Background fitness, eco-evolutionary feedbacks and the Hawk-Dove game.

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Abstract

This paper further develops work from a previous article which introduced a new way of modelling evolutionary game models with an emphasis on ecological realism, concerned with how ecological factors determine payoffs in evolutionary games. The current paper is focused on the impact of selectively neutral factors (i.e. those that are the same for all strategies), such as background fitness and a neutral density dependence on game dynamics. In the previous paper background mortality was modelled by post-reproductive mortality describing aggregated mortality between game interactions. In this paper a novel approach to the modelling of background fitness, based on different occurrence rates (intensities) of game interactions and background events is presented. It is shown that the new method is more realistic and natural for dynamic models than the method used in the previous paper. The previous method in effect produces biased trajectories, but it is compatible with the new approach at the restpoints. Also in this paper a rigorous stability analysis of the restpoints of the dynamics is presented. It is shown that the stability or instability of the restpoints, can be explained by a mechanism of eco-evolutionary feedback. The results obtained are illustrated by a Hawk-Dove game example.

keywords: evolutionary game, replicator dynamics, background fitness, density dependence

1 Introduction

In a previous paper (Argasinski and Broom 2012) a novel approach to evolutionary game modelling was presented. The new approach is focused on ecological realism, falsifiability of the models and a mechanistic interpretation of the obtained results. The main goal was to express individual fitness in terms of the demographic parameters. This will allow us to describe the parameters of the models, such as "costs" and "benefits", by clear and measurable parameters (mortality and fecundity) instead of an abstract, undefined "fitness". This is realized by the explicit application of two payoff functions describing the mortality and the fecundity, instead of one fitness function describing the excess from the mean Malthusian growth rate. The new approach can be described as "event based" because it describes cause and effect chains of underlying interaction events. For example mortality can act on adult individuals before or after reproduction. An important aspect shown by these results is that some properties known from classical evolutionary game theory (Maynard Smith 1982, Hofbauer and Sigmund 1988 and 1998) such as the independence of the replicator dynamics from the background fitness are not satisfied in the new approach. The general framework presented in Argasinski and Broom (2012) is illustrated by use of a Hawk-Dove game example, a classical application of game theoretic methods in evolutionary biology. This example clearly shows that the classical Hawk-Dove game which can be found in textbooks is seriously oversimplified. This emphasizes the importance of selectively neutral factors (i.e. those that
are the same for all strategies), such as background fitness and the impact of neutral density dependence in game theoretic models. Both of these aspects were present in Argasinski and Broom (2012) but are not rigorously analyzed there. They are the subject of this paper. We now present a brief introduction to both problems.

1.1 Background fitness

Traditionally, background fitness is interpreted as some constant (or function) added to the payoffs of all strategies which vanishes from the continuous replicator equations. This is a transfer of the background payoff concept, from the classical game theory to the evolutionary game theory. In Argasinski and Broom (2012) this approach was generalized for both mortality and fertility payoffs to show how selectively neutral elements (i.e. the same for all strategies) of the respective payoff functions act on the overall dynamics. This was realized by adding a constant $W_b$ to the fertility function and multiplying by constants $d$ and $m$, respectively, pre- and post-reproductive mortality functions. It was shown there that only pre-reproductive mortality can be interpreted as selectively neutral because it affects only the rate of convergence but does not alter the phase portraits of the dynamics. However, the post-reproductive mortality $m$ (in the further sections this will be labelled $m_1$ to distinguish from the alternative approach) and background fertility $W_b$ affects the form of the replicator equations and the game theoretic structure. In addition the Hawk-Dove example has shown that factors described by those parameters can be very important for the realism of the models. Without background mortality, individuals die only as a result of the game interaction. In the Hawk Dove game this leads to the hidden assumption that Doves are immortal, because only Hawks fight and suffer mortality due to their injuries. Thus, background mortality parameters should be incorporated in the models and this topic is extremely important. In the previous paper the mathematical aspects of the inclusion of such parameters were analyzed as the consequences of the generalization of the classical approach. However, a question arises on the adequacy of the implemented solutions, which are a simple extension of the classical theory, from the biological point of view. We discuss this topic more in Section 3. The next section contains an application of this approach, since density dependent juvenile mortality is an example of the multiplicative selectively neutral element of the fertility function.

1.2 Neutral density dependence as an effect of limitation of the population size

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 was taken into consideration. The specific case of selectively neutral density dependence was analyzed in Argasinski and Kozłowski (2008). There it was shown that density dependence can act as a
juvenile mortality driven by the availability of nest sites where newborns can settle (it is described as the logistic suppression coefficient \((1 - n/K)\), where \(K\) is the carrying capacity). In effect differences in fertility are suppressed. In the basic approach to evolutionary games where the payoff function describes the "fitness" of different strategies, this mechanism affects only the pace of convergence, while the phase portraits remain the same.

However, in the more realistic approach presented by Argasinski and Broom (2012), which this paper is a continuation of, selectively neutral density dependence has serious consequences, because it affects the impact of differences in fertility among different strategies on overall fitness including differences in mortality. In that paper it was shown that under the influence of neutral density dependence, the behavior 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 a stationary manifold. In addition, the equation on the population size leads to another stationary manifold being the function of the population composition. Thus, the global stationary states are intersections of these manifolds, which can be stable or unstable. In effect new behaviours can emerge, for example additionally to the stable mixed equilibrium, simultaneously a stable pure Hawk solution can emerge (Argasinski and Broom, 2012). The additional stable restpoint is caused by neutral density dependence.

This is related to the concept of the stationary density surface (Cressman et al. 2001, Cressman and Garay 2003), assuming that the population size traces the equilibrium value determined by the strategy frequencies. In the case of selectively neutral density dependence this surface is stable, because it is an outcome of the single equation on the population size (Argasinski and Kozłowski 2008, Argasinski and Broom 2012). In Argasinski and Broom (2012) the assumption of population size equilibrium was used to simplify the system, by substituting for the population size with the equilibrium value of the size equation into the frequency equations. This assumption is reasonable from the ecological point of view, however the role of both manifolds in the dynamics was not rigorously analyzed. Therefore, it is not clear if this assumption can be applied in every case and if it alters the predictions of the model or if it is just a limitation of the analysis to the neighbourhood of the stationary size manifold. In Argasinski and Broom (2012) stability analysis of intersections was performed for the simplified case of equilibrium size. This question will be analyzed in Section 4 which contains a general analysis of system stability and a mechanistic explanation of the interplay between the selection equilibrium describing the stable population composition and the ecological equilibrium describing the stable population size.
2 Some important details from the previous paper

This section contains some details from Argasinski and Broom (2012) and an equation found in that paper for the derivation of the model are:

\[ \dot{q}_i = q_i \left( 1 - \frac{n}{K} \right) \left( V_i - \sum_j q_j V_j \right) + \left( 1 - \frac{n}{K} \right) W_b (s_i - \sum_j q_j s_j) + b_1 (s_i - \sum_j q_j s_j) \right), \]

(1)

\[ \dot{n} = n \left( 1 - \frac{n}{K} \right) \left( W_b \sum_i q_i s_i + \sum q_i V_i \right) + b_1 \sum q_i s_i - 1 \right), \]

(2)

where \( q_i \) is the frequency of strategy \( i \), \( n \) the population size, \( K \) the carrying capacity (maximum environmental load, Hui 2006), \( V_i \) the fertility payoff function of the \( i \)-th strategy, \( s_i \) the pre-reproductive mortality payoff function of the \( i \)-th strategy, \( W_b \) the background fertility, and \( b_1 \) background post-reproductive mortality and mortality-fertility trade-off function:

and the equilibrium population size from (2) is

\[ \dot{n} = K \left( 1 - \frac{1 - b_1 \sum q_i s_i} {W_b \sum q_i s_i + \sum q_i V_i} \right). \]

(3)

A Hawk-Dove example was used to illustrate the above. This considered the payoff matrices \( S \) (mortality payoff) and \( F \) (fertility payoff) below

\[ S = \begin{pmatrix} H & D \\ H & s \end{pmatrix}, \]

\[ F = WP = \begin{pmatrix} H & 0.5W & D \\ H & 0.5W & 0 \end{pmatrix} \]

and so \( P = \begin{pmatrix} H & 0.5 & 1 \\ 0 & 0.5 \end{pmatrix} \)

where \( s < 1 \) is the survival probability of a fight between Hawks, and the fertility matrix containing the expected number of newborns \( W \) produced in effect from the interaction. This led to the equations:

\[ \dot{q}_h = q_h \left( \left( 1 - \frac{n}{K} \right) \left( W_b (e_1 S q_T - q S q_T) + W (e_1 S \cdot P q_T - q S \cdot P q_T) \right) + b_1 (e_1 S q_T - q S q_T) \right) \]

and

\[ \dot{n} = n \left( q S q_T W_b + q S \cdot P q_T W \right) \left( 1 - \frac{n}{K} \right) + q S q_T b_1 - 1 \right), \]

(5)

where the matrix operations are as follows:
\[ e_1 S q^T = sq_h + 1 - q_h = q_h(s - 1) + 1, \quad (6) \]
\[ e_1 S \cdot P q^T = 0.5 sq_h + 1 - q_h, \quad (7) \]
\[ q S q^T = q_h (q_h(s - 1) + 1) + (1 - q_h) = 1 - q_h^2(1 - s), \quad (8) \]
\[ q S \cdot P q^T = q_h (0.5 sq_h + 1 - q_h) + 0.5(1 - q_h)^2 = 0.5 (1 - q_h^2(1 - s)). \quad (9) \]

After calculations and the substitution \( d = 1 - s \) the following equations were obtained
\[ \dot{q}_h = q_h (1 - q_h) \left( \left(1 - \frac{n}{K}\right)(0.5W (1 - q_h d) - W_b q_h d - b_1 q_h d) \right), \quad (10) \]
\[ \dot{n} = n \left( (1 - q_h^2 d) \left( (W_b + 0.5W) \left(1 - \frac{n}{K}\right) + b_1 \right) - 1 \right). \quad (11) \]

Two rest points of this system are \( q_h = 0 \) and 1. A nontrivial rest point, which becomes the attractor manifold for the density dependent case, (for detailed calculation see Argasinski and Broom (2012) is given by

\[ \tilde{q}_h(n) = \frac{0.5W \left(1 - \frac{n}{K}\right)}{d \left( (W_b + 0.5W) \left(1 - \frac{n}{K}\right) + b_1 \right)}. \quad (12) \]

There is a stable population size if either \( \dot{n} = 0 \) or the following positive restpoint which is conditional on the actual hawk strategy frequency (describing the attractor manifold parametrized by \( q_h \))
\[ \tilde{n}(q_h) = K \left( 1 - \frac{1 - b_1 (1 - q_h^2 d)}{(W_b + 0.5W) (1 - q_h^2 d)} \right). \quad (13) \]

The intersections of the above manifolds 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
\[ \tilde{q}_h = \frac{\left(2 \frac{W_b}{W} + 1\right) d - \sqrt{\left(2 \frac{W_b}{W} + 1\right) d^2 - 4 b_1 d (1 - b_1)}}{2 b_1 d} \quad (14) \]

and the second is an invasion barrier for a stable pure Hawk equilibrium (where \( q_h \) converges to Hawk if and only if \( q_h > \tilde{q}_h \))
\[ \hat{q}_h = \frac{\left(2 \frac{W_b}{W} + 1\right) d + \sqrt{\left(2 \frac{W_b}{W} + 1\right) d^2 - 4 b_1 d (1 - b_1)}}{2 b_1 d}. \quad (15) \]
3 Problems with background fitness

In the (Argasinski and Broom 2012) to describe background mortality and fertility, a generalization of classical background fitness was applied to show the impact of the selectively neutral elements of the mortality and fertility payoff functions on the dynamics. There background fertility is some additive value $W_b$ added to the fertility functions and background mortality is expressed as a multiplicative survival $b_1 = 1 - m_1$ (index 1 was not in the original work, but is added here to distinguish this from our alternative approach introduced later) which is uniform for all strategies and does not affect the fertility. Since this mortality factor was modelled according to post-reproductive mortality combined with game-related pre-reproductive mortality, only game survivors are affected by $b_1$. Thus both coefficients appear in the growth equations as additive factors $s_i \left(1 - \frac{1}{\tau_1}\right) W_b + s_ib_1$. In the replicator dynamics they appear inside the bracket of the right side of equation as an additive factor which has the form $\left((1 - \frac{1}{\tau_1}) W_b + b_1\right)(s_i - \sum q_js_j)$. Thus, in the original equation where we have a single interaction rate $\tau_1$, the background mortality component related to $b_1$ is $\tau_1 s_i (1 - b_1) = \tau_1 s_i m_1$. This means that survivors of a game event suffer mortality $m_1$ which can be interpreted as the aggregated mortality between the contests.

However, the question arises: is this approach correct? This structure suggests that background fertility and mortality acts directly after the contest and is a last part of a causal chain started by the game. Thus in Argasinski and Broom (2012), background fitness can be viewed as a simple adjustment to all of the payoffs arising out of a single interaction. This is conventionally how background fitness is incorporated in classical evolutionary games, where for static analysis and replicator dynamics for simple matrix games the background fitness has no effect, since only differences in payoffs matter. In such simple cases, this would also be the case if background fitness was regarded as coming from a separate source, since all individuals would again receive the same reward, and so no distinction is made between these two possibilities. As was shown in Argasinski and Broom (2012) background fitness can seriously affect the dynamics. Therefore the distinction between the two types of the background fitness became important.

Especially from the point of view of the event based approach introduced in Argasinski and Broom (2012), background fitness should be rather the outcome of independent interactions not linked with a game. As was shown there all mating events can be lost due to pre-reproductive mortality, thus not only differences in fertilities but exact numbers of offspring should be analyzed in the models. Thus whilst background payoffs of the different type as discussed in Argasinski and Broom (2012) was a plausible way to first consider background fitness in our model, a more natural, and we would argue better, way is the one we shall use in this paper.
3.1 An alternative approach to background fitness based on the rate of event occurrence $\tau$

The new approach is related to the methodology used for the separation of ecological equations from selection dynamics (Cressman and Garay 2003a and 2003b, Cressman et al. 2001). However, we do not want to separate the ecological dynamics from the selection dynamics, since we believe that relationships between ecology and selection are extremely important. We want to separate the outcomes of a particular game from the outcomes of games of the other types. The effect of background fitness can be modelled more intuitively by different types of events occurring at different rates (the rate of occurrence of the $i$th type of event will be labelled $\tau_i$), which is a generalization of the approach presented in Appendix 1 of Argasinski and Broom (2012).

We can consider multiple different types of events which occur as independent Poisson processes. This will allow us to remove survivors background fitness $W_b\sum_i q_is_i$ and $b\sum_i q_is_i$ from equations (1) which will lead to the equations (20) described below. Individuals enter a game at rate $\tau_1$, whilst they perform other activities at rate $\tau_2$; we can consider a single class of all such activities, as we show below. Assume that there are several types of background activities occurring at rate $\tau_2$, and each of these events can be characterized by outcomes which include a fertility $W_i^b$ and mortality $b_i^2$ component. If the event of the $i$th type is a safe mating opportunity then the respective survival $b_i^2$ equals one. On the other hand if the event is not related to mating or reproduction but is dangerous then $W_i^b = 0$. We can calculate the outcomes of the average background event. $W_b = \sum_i \tau_i W_i^b/\tau_2$ is the average fertility per event (where $\tau_2 = \sum_i \tau_i^2$) and $b_2 = \sum_i \tau_i^2 b_i^2/\tau_2$ is the average survival probability per event (which can be called “parallel to game” mortality for distinction from post-reproductive mortality in the cause-effect chain). In effect “background events” occur at intensity $\tau_2$ and individuals involved in those events can obtain on average $W_b$ fertility and survive with probability $b_2$. Thus the general Malthusian equation will be:

$$\dot{n}_i = n_i \tau_1 V_i \left(1 - \frac{n}{K}\right) - n_i \tau_1 (1 - s_i) + n_i \tau_2 W_b \left(1 - \frac{n}{K}\right) - n_i \tau_2 (1 - b_2). \quad (16)$$

If $\tau_1 = \tau_2$ then after change of the timescale $\tilde{t} = t/\tau_1$ (see Appendix 1 of Argasinski and Broom, 2012) both of them vanish, if not then $\tau_1$ vanishes and $\tau_2$ transforms into $\theta = \frac{\tau_2}{\tau_1}$. Then the Malthusian equation will be:

$$\dot{n}_i = n_i \theta W_b + n_i V_i \left(1 - \frac{n}{K}\right) - n_i \theta (1 - b_2) - n_i (1 - s_i) \quad (17)$$

$$ = n_i \left[\theta W_b + V_i \left(1 - \frac{n}{K}\right) - \theta (1 - b_2) - (1 - s_i)\right]. \quad (18)$$

As we see below in equation (20), $\theta W_b$ and $\theta (1 - b_2)$ vanishes from replicator equations for the frequencies, thus in this case we obtain replicator equations
from the original paper (1) without background fitness (i.e. $W_b = 0$ and $b_1 = 1$ but they are present in the size equation:

$$\dot{n} = n \left[ \left( 1 - \frac{n}{K} \right) \left( \theta W_b + \sum_i q_i V_i \right) - \theta(1 - b_2) - \left( 1 - \sum_i q_i s_i \right) \right]. \quad (19)$$

Parameters $\tau_2$, $W_b$ and $b_2$ can be biologically justified and can even be functions of other parameters (for example from other types of game). However, if we need only some background "noise" without particular justification, to add realism to our model, we can simplify the notation. Because parameters $W_b$ and $b_2$ never occur without the ratio between intensities $\theta$, we can simplify this by substitution $\Phi = \theta W_b$ and $\Psi = \theta(1 - b_2)$ and we obtain the following system:

$$\dot{q}_i = q_i \left( \left( 1 - \frac{n}{K} \right) \left( V_i - \sum_j q_j V_j \right) + \left( s_i - \sum_j q_j s_j \right) \right), \quad (20)$$

$$\dot{n} = n \left[ \left( 1 - \frac{n}{K} \right) \left( \Phi + \sum_i q_i V_i \right) + \sum_i q_i s_i - 1 - \Psi \right], \quad (21)$$

where equation (21) follows directly from equation (19), and equation (20) is obtained using equations (18), (19) and the fact that $\dot{q}_i = (n_i / n) = (\dot{n}_i n - \dot{n} n_i) / n^2$. The stable population size is given by

$$\left( 1 - \frac{n}{K} \right) \left( \Phi + \sum_i q_i V_i \right) + \sum_i q_i s_i - 1 - \Psi = 0 \quad (22)$$

which leads to

$$1 - \frac{n}{K} = \frac{\Psi + 1 - \sum_i q_i s_i}{\Phi + \sum_i q_i V_i}, \quad (23)$$

while in Argasinski and Broom (2012) we have

$$1 - \frac{n}{K} = \frac{1 - b_1 \sum_i q_i s_i}{W_b \sum_i q_i s_i + \sum_i q_i V_i}. \quad (24)$$

Thus the new approach presented above is somewhat simpler than the original equations. A question arises about the relationship between both approaches. Is the original approach a simplified approximation of the more detailed new approach?
3.2 A comparison of the new approach with the approach from the previous paper

Let us compare the general size equations using the different approaches to the background mortality, where $b_1$ is the approach used in Argasinski and Broom (2012) and $b_2$ is the new approach from the section above. For the new approach we have

$$
\dot{n}_i = n_i V_i \left(1 - \frac{n_i^n}{K^n}\right) - n_i (1 - s_i) - n_i \theta (1 - b_2) \tag{25}
$$

whereas the equation for the original approach was

$$
\dot{n}_i = n_i V_i \left(1 - \frac{n_i^n}{K^n}\right) - n_i (1 - s_i) - n_i s_i (1 - b_1). \tag{26}
$$

Thus the decay rates constituted by mortality terms in equations (25) and (26) are

$$
E_1 = -(1 - s_i) - \Psi \tag{27}
$$

for the new approach, and

$$
E_2 = -(1 - s_i) - s_i m_1 \tag{28}
$$

for the original approach, where $m_1 = 1 - b_1$ and $\Psi = \theta m_2 = \theta (1 - b_2)$. Thus equality of the decay rates of both approaches $E_1 = E_2$ implies the condition

$$
s_i m_1 = \theta m_2 \tag{29}
$$

which cannot be satisfied for every $i$. Now, let us focus on the relationship between both approaches. They are certainly not equivalent, however we are interested in when the approaches are compatible.

3.2.1 When are both approaches compatible?

Relationship (29) cannot be satisfied in most of the cases, but other methods can be applied to show conditions when the original approach can be treated as an approximation of the more detailed new approach. Suppose that the game interaction happens at rate $\tau_1$ and background death events with rate $\nu$ (during that event an individual dies with probability 1). Setting $\gamma = \nu/\tau_1$ using the basic properties of the Poisson process, the survival probability is $b_1 = \frac{1}{1 + \gamma}$ since survival occurs if a new contest comes before death. It is easy to show that both approaches are not compatible in the general case. But under assumption of ecological equilibrium (stable population size) some relationships between first approach as the approximation of the second approach to the background mortality can be derived. They are summarized by following theorem
Theorem 1
If we assume that $b_1 = \frac{1}{1 + \Psi}$ (or respectively $m_1 = \frac{\Psi}{1 + \Psi}$) and the population size equilibrium condition (23) is satisfied then:

a. The stationary frequency points for both approaches are the same.

b. The rate of the dynamics in the first approach equals the rate of the second approach divided by $1 + \Psi$.

c. The stationary population sizes are different, with the value of $(1 - \frac{n}{K})$ in the first approach equalling that of $(1 - \frac{n}{K}) / (1 + \Psi)$ in the second approach.

For a proof see Appendix 1.

Thus it is possible to approximate independent background mortality by post-reproductive mortality related to the game event, describing the aggregated mortality caused by independent background events occurring between game interactions. The question arise about usefulness of this method. This will be shown in section 5 by Hawk-Dove game example.

4 Selectively neutral density dependence and the concept of the eco-evolutionary feedbacks.

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 on 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 stationary manifolds obtained by calculation of the zero points of the equations.

Argasinski and Broom (2012) contains the derivation of both stable manifolds $\hat{q}(n)$, and $\hat{n}(q)$ (described more fully below) for the Hawk-Dove example, and the calculation of their intersections. However, a rigorous stability analysis is limited to the case when the system is in ecological equilibrium (Theorem 2 of that paper). In this section the general result will be provided for games with two strategies. We can imagine more complicated two-strategy systems with multiple frequency dependent mortality and fertility stages (see section 3 in Argasinski and Broom, 2012), but all of them can be presented in the general form

$$\dot{q} = q \left( (1 - \frac{n}{K}) W_1(q) - M_1(q) \right), \quad (30)$$

$$\dot{n} = n \left( W_2(q) \left( 1 - \frac{n}{K} \right) - M_2(q) \right), \quad (31)$$

where $W_1(q) = W_i - \bar{W}$ and $M_1(q) = m_i - \bar{M}$ describe the frequency dependent functions from the bracketed terms, while $W_2(q) \geq 0$ and $M_2(q) \geq 0$, since fecundities and mortalities are always non-negative. It is possible that
there exist stable manifolds \( \tilde{q}(n) \) and \( \tilde{n}(q) \) defined as follows. Expressing \( q \) as a function of \( n \), the stable manifold \( \tilde{q}(n) \) is defined by the value of \( q \) for which the right-hand side of equation (30) is 0 for any given \( n \) (it is possible that there is more than one such solution, and so more than one such manifold). Similarly, expressing \( n \) as a function of \( q \), the stable manifold \( \tilde{n}(q) \) is defined by the value of \( n \) for which the right-hand side of equation (31) is 0 for any given \( q \).

Now consider the phase space \( q \times n \), consisting of all possible values of \( q \) and \( n \). On the manifolds \( \tilde{q}(n) \) and \( \tilde{n}(q) \) the right-hand side of the equations (30) and (31) respectively equals zero, and these manifolds divides the phase space into regions of growth and decline for \( q \) and \( n \). When the right-hand side of equation (30) is negative we have that \( q(n) > \tilde{q}(n) \) is the region of decline for \( q \).

We note that in the method presented in Argasinski and Broom (2012), the stable population size \( \tilde{n}(n) \) was substituted into the right hand side of equation (30). Substitution of \( \tilde{n}(q) \) into \( \tilde{q}(n) \) leads to the inequuality \( q < (>) \tilde{q}(\tilde{n}) \) describing the regions of growth (decline) of \( q \) lying on the stable size manifold \( \tilde{n}(q) \). In Argasinski and Broom (2012) the inequality \( q \leq \tilde{q}(\tilde{n}) \) has the form of a quadratic equation. Zeros of this equation are intersections of the stable size and stable frequency manifolds. 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 stable density manifold. Below, by application of standard linearization methods we will show that those characteristics can be extended to the neighbourhood of the stable density manifold:

**Theorem 2** If for the system described by equations (30) and (31), stable manifolds \( \tilde{q}(n) \) and \( \tilde{n}(q) \) exist, then any intersection of the manifolds is an equilibrium point, where:

a) if this equilibrium is unstable on the stable size manifold then it is unstable.

b) if this equilibrium is stable on stable size manifold then it is a local attractor if and only if the stable frequency manifold’s slope is not sufficiently steeply decling in the direction of the strategy favoured by high population size.

For a proof see Appendix 2.

Thus we can mechanistically interpreted 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). Let us denote the stationary frequencies of the system (which are the frequencies at the intersections of the manifolds \( \tilde{q}(n) \) and \( \tilde{n}(q) \)) here by \( q_{\text{stat}} \). Perturbation in \( q \) induces convergence towards the respective stable size \( \tilde{n}(q_{\text{pert}}) \) lying on the stable density manifold \( \tilde{n}(q) \) which determines the respective frequency attractor \( \tilde{q}(\tilde{n}(q_{\text{pert}})) \) on the stable frequency manifold.
\( \dot{q}(n) \). If \( |\dot{q}(\tilde{n}(q_{\text{pert}})) - q_{\text{stat}}| < |q_{\text{pert}} - q_{\text{stat}}| \) then negative feedback is induced in a sense that dynamics chase \( \tilde{q}(\tilde{n}(q_{\text{pert}})) \) towards \( q_{\text{stat}} \). In effect \( q_{\text{stat}} \) is stable. On the other hand, if \( |\dot{q}(\tilde{n}(q_{\text{pert}})) - q_{\text{stat}}| > |q_{\text{pert}} - q_{\text{stat}}| \) then a positive feedback is induced and the attractor escapes from \( q_{\text{stat}} \). In effect \( q_{\text{stat}} \) is unstable. See Figure 1 for an illustration. The above general notions can be applied in our Hawk-Dove example, as we show below.

### 4.1 Formulation of the updated Hawk-Dove game example

We now illustrate the general concepts from the sections above illustrated with the example of the Hawk-Dove game. The frequency equations will be the same as (10) with \( W_b = 0 \) and \( b_1 = 1 \), but the size equation will be different because the terms \( \Phi \left( 1 - \frac{n}{K} \right) \) and \(-\theta(1 - b_2) (-\Psi)\) should be added. This will lead to the application of the system (20) and (21) and the payoff functions derived from Hawk-Dove game matrices \( S \) and \( P \). The system will have the form:

\[
\dot{q}_h = q_h \left( 1 - \frac{n}{K} \right) W \left( e_1 S \cdot P q^T - q S \cdot P q^T \right) + \left( e_1 S q^T - q S q^T \right) \\
\dot{n} = n \left( \Phi + q S \cdot P q^T W \right) \left( 1 - \frac{n}{K} \right) + q S q^T - 1 - \Psi. 
\]

After substitution of (6,7,8,9) and respective calculations and auxiliary substitution \( d = 1 - s \) we obtain:

\[
\dot{q}_h = q_h \left( 1 - q_h \right) \left( 0.5W \left( 1 - q_h d \right) \left( 1 - \frac{n}{K} \right) - q_h d \right), \\
\dot{n} = n \left( \Phi + \left( 1 - q_h^2 d \right) 0.5W \right) \left( 1 - \frac{n}{K} \right) - q_h^2 d - \Psi. 
\]

Note that without background fertility \( W_b \) the above system collapses to:

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

\[
\dot{n} = n \left( 1 - q_h^2 d \right) \left( 0.5W \left( 1 - \frac{n}{K} \right) \right) + 1 - 1 - \Psi. 
\]

In Argasinski and Broom (2012) the above system was simplified using the assumption that equation (37) is in the equilibrium and that evolution of the system is limited to be on the stable density manifold. Therefore, we can simplify also the new system by substitution of the equilibrium of (37) which is

\[
\tilde{n}(q_h) = K \left( 1 - \frac{1 + \Psi - (1 - q_h^2 d)}{0.5W \left( 1 - q_h^2 d \right)} \right),
\]

13
to the logistic suppression coefficient in (36) which leads to
\[ \dot{q}_h = q_h (1 - q_h) \left( 1 - q_h d \left( \frac{1 + \Psi - (1 - q_h^2 d)}{1 - q_h^2 d} \right) - q_h d \right). \] (39)

4.2 Relationships between new formulation of the Hawk-Dove example and the previous paper.

Following the previous section and considering background fertility \( W_b \), the approach from Argasinski and Broom (2012) and the new approach are not compatible and the new approach is more realistic, general and mathematically simple. Let us now consider the problem of the background mortality which is a bit more complicated. For simplicity we remove background fertility with the assumption that \( W_b = 0 \). Thus equations (10) and (11) for the Hawk-Dove model become:
\[ \dot{q}_h = q_h (1 - q_h) \left( 1 - q_h d \left( 0.5W (1 - q_h^2 d) \left( 1 - \frac{n}{K} \right) - b_1 q_h d \right) \right), \] (40)
\[ \dot{n} = n \left( (1 - q_h^2 d) \left( 0.5W \left( 1 - \frac{n}{K} \right) + b_1 \right) - 1 \right). \] (41)

In the previous sections it was shown that the new system \((38,39)\) will produce different trajectories to the model from the previous paper relating to \((40,41)\). However, after substitution of the equilibrium population size \((13)\) to limit the system to the stable density manifold, we obtain the equation:
\[ \dot{q}_h = q_h (1 - q_h) \left( 1 - q_h d \left( \frac{1 - b_1 (1 - q_h^2 d)}{1 - q_h^2 d} \right) - b_1 q_h d \right) \] (42)
and the respective population size:
\[ \tilde{n}(q_h) = K \left( 1 - \frac{1 - b_1 (1 - q_h^2 d)}{0.5W (1 - q_h^2 d)} \right). \] (43)

As was shown in Theorem 1 in this case the system \((42,43)\) can be regarded as a biased approximation of the new system \((38,39)\). Then \( b_1 \approx \frac{1}{1 + \theta(1 - b_2)} \) (or \( m_1 \approx \frac{\Psi}{1 + \Psi} \)). However, the obtained equations are not simpler. The removal of \( \theta \) under assumption of stable population size seems not to be profitable because frequency conditions will be more complex \( (b_1 \text{ instead of } 1) \).
5 Numerical examples and their analysis

This section contains numerical simulations of the updated Hawk-Dove game \([34,35]\) to show the dynamics induced by the eco-evolutionary feedback mechanism. For simplicity we remove the background fertility \(\Phi\). In Theorem 2 the local stability of intersections of the stable manifolds was proved. However the trajectories of the population away from this intersection 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 this paper by the phenomenon of the eco-evolutionary feedback. In this section we will focus on the relationship between the trajectories, population size and the geometry of the stable manifolds \(\tilde{q}(n)\) and \(\tilde{n}(q)\), to reveal new details of this process which were not shown in Argasinski and Broom (2012).

5.1 Phase portraits of the dynamics

In Argasinski and Broom (2012) results of the numerical simulations emphasized the role of the intersections of both manifolds. In this paper we want to show the trajectories prior to convergence. To emphasize the role of both manifolds, in Figures 2-4, 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 limited by both manifolds which are very close to each other in the cases when intersections are relatively close (see for example Figure 5). Some of the numerical simulations support the intuition that the dynamics converge to the close neighbourhood of the stable density surface and then trace the equilibrium size value (Fig.2). In this case the assumption from Argasinski and Broom (2012) of the population taking the stable size for given frequency is justified. However, this happens when both manifolds are placed at relatively high densities. At lower densities the trajectory does not reach a strict neighbourhood of the stable density surface (Fig.3). At very low densities the trajectory converges closer to the stable frequency manifold (Fig 4). We note that this effect is suppressed with population growth. In some cases the trajectory converges to the close neighbourhood of the stable frequency manifold and traces it nearly to the equilibrium (Fig.5). Thus, the assumption that frequency selection occurs on the stable density surface can sometimes be seriously wrong. In the general case the geometry of both manifolds 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 toward the stable density surface while at lower densities there is a stronger attraction toward the stable frequency manifold. Therefore, the ecological equilibrium assumption is a simplification of the entire problem, sometimes with results clearly different to those of the general model. The differences between both approaches will be analyzed in the
next section.

5.2 Comparison of examples with and without assumption of the stable population size starting from the same initial conditions.

The stable population size assumption can be very strong. Figures 6 and 7 show a comparison of the trajectories of the general and simplified models. The main difference is that the rate of convergence is accelerated in the simplified model. Another important difference is that in the general model the density dynamics does not "trace" the equilibrium value, but rather "chases" it. This is reasonable, because ecological equilibrium implies zero growth rate, which is in contradiction with the rapid growth of the population size shown by the trajectory. Thus in the general model there is inertia which is suppressed in the simplified model where density dynamics is forced to trace the equilibrium conditional on the current population composition. Figure 7 shows the dynamics of extinction. In the general model frequency dynamics follows the stable frequency manifold due to very low densities, while in the simplified model, again, the trajectory is forced to trace the stable density surface.

Another interesting aspect is shown by the density dynamics in both variants. In the general model the rate of population decline significantly decreases with the population size (the distance from the stable density surface increases) and smoothly converges to the restpoint 0. In the simplified model the trajectory stabs through the 0 level and takes negative values, since it is constrained to follow the stable density surface, and this assumption becomes increasingly unreasonable as the 0 level is approached (clearly equation (31) can yield negative values for some parameters are values of $q_h$). This shows that in the simplified model the density dynamics is biased. Comparing both approaches, in the simplified system only the bracket describing the average per capita growth rate is taken into consideration instead of the overall dynamics. In addition, the chosen population size should zero this bracket, which is also an unrealistic assumption. However, as was shown by numerical examples, at high densities, the trajectory can nearly trace the equilibrium. Thus this method is a simplified approximation appropriate under certain conditions, not necessarily the limitation of initial values equivalent to the general model.

6 Discussion

Results presented in this paper show the importance of two selectively neutral factors: background fitness and neutral density dependence in the selection dynamics.
Background fitness is the first factor that affects the outcomes of the model, and should be realistically modelled. The natural approach is to use the different interaction rates (intensities) describing fractions of individuals involved in game interactions and some particular type of background event resulting in additional fertility and mortality. This new approach is more realistic and provides an easier mechanistic interpretation than the method used in Argasinski and Broom (2012), which was inspired by the traditional approach to background fitness. The selectively neutral elements of the payoff functions are good tools to model the factors linked with the particular game event, which is clearly shown by the example of the density dependent juvenile mortality. However, background events should be described in the dynamics by different intensities and their own specific neutral "payoff" functions.

Using neutral density dependence, the results introduced in Argasinski and Broom (2012) have been clarified and improved. We have proved that claims on the local stability of the manifold intersections on the stable density surface can be extended to the neighbourhood of that surface. In effect, the general method of finding intersections of stable manifolds has been mathematically justified and generalized. The phenomenon of stability and instability of the intersections was mechanistically explained by the concept of eco-evolutionary feedbacks. 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. The new approach is related to current development in evolutionary theory focused on relationships of selection processes with ecological factors (Schoener 2011, Morris 2011, Pelletier et al. 2009).

Numerical simulations show a variety of behaviours. Some of these are against intuition based upon the dynamics concentrated on frequencies occurring on the stable density manifold. At low densities there is a stronger attraction towards the stable frequency manifold. 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 manifolds are important for the dynamics.

There are possible simplifications of the general model used in Argasinski and Broom (2012). One simplification relies in the reduction of the dimension of the problem by substituting the population size equation by its equilibrium value. However, results from this paper, especially numerical simulations, clearly show that this is. A simplified approximation of the general model which is seriously biased unless the population is at relatively high densities. Under the assumption of ecological equilibrium, background mortality can be approximated by a game interaction related post-reproductive mortality describing the aggregated background mortality between game interactions. In effect rates of occurrence (intensities) can be removed from the equations. However, it is not useful for
the dynamic models, because the equations obtained are more complex than before and their trajectories are seriously altered. Only restpoints are compatible. Also the interpretation of the background mortality described as the post-reproductive mortality is problematic in the dynamic context.

However, it does not mean that this approach is completely useless. If we are not interested in explicit modelling of the dynamics but interested only in the restpoints, the original approach is more natural because the underlying strategic reasoning is expressed in terms of outcomes of some events measured as fertilities and mortalities instead of the abstract rates such as Ψ. Thus the approximation of the background mortality from the original approach can be useful in static analysis which is equivalent to finding zeros of the right sides of the replicator equations.

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Appendix 1

Proof of theorem 1:

a) and b) The replicator equations of the original approach (Argasinski Broom 2012) are given by

\[
\dot{q}_i = q_i \left( \left( V_i - \sum_j q_j V_j \right) \left( 1 - \frac{n}{K} \right) + b_1 (s_i - \sum_j q_j s_j) \right)
\]

(44)

and for \( W_b = 0 \) (equation 24) we have the form

\[
1 - \frac{n}{K} = 1 - \frac{b_1 \sum_i q_i s_i}{\sum_i q_i V_i}.
\]

(45)

After substitution of the population size equilibrium (45) to (44) we have:

\[
\dot{q}_i = q_i \left( \left( V_i - \sum_j q_j V_j \right) \frac{1 - b_1 \sum_i q_i s_i}{\sum_i q_i V_i} + b_1 (s_i - \sum_j q_j s_j) \right)
\]

(46)

and after substitution of \( b_1 = \frac{1}{1 + \Psi} \) we have

\[
\dot{q}_i = \frac{q_i}{1 + \Psi} \left( \left( V_i - \sum_j q_j V_j \right) \frac{\Psi + 1 - \sum_i q_i s_i}{\sum_i q_i V_i} + (s_i - \sum_j q_j s_j) \right).
\]

(47)
Thus $b_1$ affects only the rate of convergence and manifold intersections will be the same as in the new method presented in this paper.

c) Application of this approach leads to following differences:

stable sizes:

\[
(1 - \frac{n}{K}) = \frac{1 - s_i + \Psi}{V_i} \quad \text{for the new approach}
\]

\[
(1 - \frac{n}{K}) = \frac{1 - b_1 s_i}{V_i} \quad \text{for the original approach.}
\]

After substitution of $b_1 = \frac{1}{1 + \theta(1 - b_2)}$ we have:

\[
(1 - \frac{n}{K}) = \frac{1 - s_i}{1 + \Psi} = \frac{1 - s_i + \Psi}{V_i} = \frac{1 - s_i + \Psi}{V_i} b_1.
\]

The difference is that denominator of logistic bracket is multiplied by $(1 + \Psi)$.

**Appendix 2**

Proof of theorem 2:

We can present our system in the form:

\[
f(n, q) = \frac{dn}{dt} = n \left( W_2(q) \left( 1 - \frac{n}{K} \right) - M_2(q) \right), \quad (48)
\]

\[
g(n, q) = \frac{dq}{dt} = q \left( W_1(q) \left( 1 - \frac{n}{K} \right) - M_1(q) \right) \Rightarrow \quad (49)
\]

\[
g(n, q) = \frac{dq}{dt} = q(1 - q) \left( W_3(q) \left( 1 - \frac{n}{K} \right) - M_3(q) \right), \quad (50)
\]

where $W_2(q) \geq 0$, $M_2(q) \geq 0$, $W_3(q) = W_1(q)/(1-q)$ and $M_3(q) = M_1(q)/(1-q)$.

The fact that equation (49) can be written in the form of equation (50) can be seen by noting that $\frac{dq}{dt} = -\frac{d(1-q)}{dt}$, which can also be written in analogous form with a factor of $(1-q)$.

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 derivatives are

\[ f_n(n, q) = W_n(q) \left( 1 - \frac{n}{K} \right) - M_n(q) - n \frac{W_n(q)}{K} \]
\[ f_q(n, q) = n \left( W_n'(q) \left( 1 - \frac{n}{K} \right) - M_n'(q) \right) \]
\[ g_n(n, q) = -\frac{(1 - q)qW_n(q)}{K} \]
\[ g_q(n, q) = \frac{1 - q}{W_n(q)} \left( 1 - \frac{n}{K} \right) - M_n(q) - n \frac{W_n(q)}{K} \]

where \( W_n'(q) \) is the derivative of \( W_n(q) \) w.r.t. \( q \), and similarly \( M_n'(q) \) is the derivative of \( M_n(q) \) w.r.t. \( q \), for \( i = 1, 2, 3 \).

After substitution of the stationary points we have

\[ f_n(\hat{n}, \hat{q}) = -\hat{n} \frac{W_n(\hat{q})}{K} \leq 0 \]
\[ f_q(\hat{n}, \hat{q}) = \hat{n} \left( W_n'(\hat{q}) \left( 1 - \frac{n}{K} \right) - M_n'(\hat{q}) \right) \]
\[ g_n(\hat{n}, \hat{q}) = -\frac{\hat{q}(1 - \hat{q})W_n(\hat{q})}{K} \leq 0 \]
\[ g_q(\hat{n}, \hat{q}) = \hat{q}(1 - \hat{q}) \left( W_n'(\hat{q}) \left( 1 - \frac{n}{K} \right) - M_n'(\hat{q}) \right) \]

The eigenvalues of the Jacobian are found as follows.

\[ \begin{vmatrix} f_n(\hat{n}, \hat{q}) - \lambda & f_q(\hat{n}, \hat{q}) \\ g_n(\hat{n}, \hat{q}) & g_q(\hat{n}, \hat{q}) - \lambda \end{vmatrix} = \lambda^2 + A\lambda + B \] (51)

where \( A = -(f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q})) \) and \( B = f_n(\hat{n}, \hat{q})g_q(\hat{n}, \hat{q}) - f_q(\hat{n}, \hat{q})g_n(\hat{n}, \hat{q}) \).

Thus

\[ \lambda_{1,2} = \frac{-A \pm \sqrt{A^2 - 4B}}{2} \]

For stability we need either two negative eigenvalues or two complex eigenvalues with negative real parts. This occurs when \( A > 0 \) and \( B > 0 \).

\( B > 0 \) 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

\[ \frac{d\hat{n}(q)}{dq} > \frac{d\hat{q}(q)}{dq} \]

where \( \hat{q}(q) \) expresses the stable frequency manifold in terms of \( n \) as a function of \( q \) (this is possible as there is a 1-1 correspondence between \( n \) and \( q \), at least in the vicinity of a root). For example in Figure 3 we see that the slope of the stable density manifold with respect to \( q \) is less than that of the stable frequency manifold at the first root (both are negative and the former is declining more quickly), so that this root is unstable. At the second root the order of the derivatives is reversed, so that the root may be (and in fact is, see below) stable.
The second condition for stability is \( A > 0 \). This 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 of frequency independent models. Thus, for example, the Hawk-Dove game which has a mixed ESS for its frequency-independent version (the classical game) automatically satisfies this condition.

In general, for our model

\[
f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q}) < 0 \Rightarrow -\frac{f_n(\hat{n}, \hat{q})}{g_n(\hat{n}, \hat{q})} + g_q(\hat{n}, \hat{q}) < 0\]

if \( g_n(\hat{n}, \hat{q}) \) is negative (positive), i.e. if \( W_1(\hat{q}) \) is positive (negative). Thus the stable frequency manifold’s slope is not sufficiently steeply declining in the direction of the strategy favoured by high population size.

Now let us compare this solution with the case from Argasinski and Broom (2012) where the population size was assumed to take its equilibrium value. This means that equation (48) is set to 0, giving equation (49) as

\[
g(n, q) = \frac{dq}{dt} = q \left( W_1(q) \frac{M_2(q)}{W_2(q)} - M_1(q) \right). \tag{54}
\]

Differentiating with respect to \( q \) at an equilibrium value \( \hat{q} \) will give stability within the manifold if and only if the derivative is negative. Thus such a root is stable if

\[
-\frac{\hat{q} W_1(\hat{q})}{\hat{n} W_2(\hat{q})} f_q(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q}) < 0 \Rightarrow \tag{56}
\]

which is identical to \( B > 0 \) since \( f_n(\hat{n}, \hat{q}) < 0 \).

Thus any solution using the stable population size assumption of Argasinski and Broom (2012) which is unstable is automatically unstable in the vicinity of the root for the general game, and any solution that is stable under that assumption is stable provided that the slope of the frequency manifold satisfies the stated extra condition.

end of the proof
| Symbol | Meaning |
|--------|---------|
| $W_b$  | background fertility (number of offspring) |
| $q_h(n)$ | stable frequency manifold |
| $m$ -  | background post-reproductive mortality |
| $\tilde{n}(q_h)$ | stable density manifold |
| $K$    | carrying capacity (maximal environmental load) |
| $\tau_1$ | rate of occurrence (intensity) of the game event |
| $n$    | population size |
| $\tau_2$ | rate of occurrence of the background event |
| $q_i$  | frequency of the $i$-th strategy |
| $m_1 = 1 - b_1$ | background mortality of Argasiński and Broom (2012) |
| $V_i = \sum_j q_j s_i(e_j) W_i(e_j)$ | mortality-fertility trade-off function |
| $\theta$ | $= \frac{\tau_2}{\tau_1}$ |
| $s_i$  | survival probability of the $i$-th strategy |
| $\Phi = \theta W_b$ | rate of the average background fertility |
| $S$    | mortality payoff matrix |
| $\Psi = \theta(1 - b_2)$ | rate of the background mortality |
| $F = WP$ | fertility payoff matrix |
| $E_2$  | decay rate from Argasiński and Broom (2012) |
| $d = 1 - s$ | probability of death |
| $E_1$  | decay rate of the new approach |

Table 1: List of important symbols
FIGURE CAPTIONS

Figure 1 Presentation of the eco-evolutionary feedback mechanism. Positive or negative feedback is induced by the position of the density and frequency attractors $\tilde{n}(q_{\text{pert}})$ and $\tilde{\tilde{n}}(q_{\text{pert}}))$ towards the stationary point (intersection) $q_{\text{stat}}$. 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 stable density manifold is much stronger than attraction towards the stable frequency manifold.

Figure 2 Initial conditions $q_h(0) = 0.2$ and $n(0) = 147$. Model parameters: $W = 7$, $d = 0.5$, $\Psi = 0.01$. The trajectory converges to the very close neighbourhood of the stable density surface and follows it converging to the mixed equilibrium $\tilde{q}_h = 0.0202$. The Hawk invasion barrier is $\tilde{\tilde{q}}_h = 0.9897$. Thus in a stable mixed equilibrium there is approximately one Hawk per 50 Doves and Hawks can invade a population if their number exceeds 100 per single Dove.

Figure 3 Initial conditions $q_h(0) = 0.6$ and $n(0) = 147$. Model parameters: $W = 7$, $d = 0.8$, $\Psi = 0.06$. At lower densities convergence to the stable density surface is not strong. The stable frequency manifold is passed by the trajectory. The mixed equilibrium is $\tilde{q}_h = 0.0762$, while the Hawk invasion barrier is $\tilde{\tilde{q}}_h = 0.9837$ is still small.

Figure 4 Initial conditions $q_h(0) = 0.89$ and $n(0) = 147$. Model parameters: $W = 0.8$, $d = 0.5$, $\Psi = 0.01$. In this case, at the beginning the trajectory passes the stable density surface and converges to the neighbourhood of the stable frequency surface, but then the trajectory leaves it slowly converging to the density surface. The mixed equilibrium is $\tilde{q}_h = 0.0202$, while the Hawk invasion barrier is $\tilde{\tilde{q}}_h = 0.9897$.

Figure 5 Initial conditions $q_h(0) = 0.2$ and $n(0) = 20$. Model parameters: $W = 3$, $d = 0.9$, $\Psi = 0.4$. In this case the trajectory converges to the very close neighbourhood of the stable frequency surface and follows it almost to the mixed equilibrium $\tilde{q}_h = 0.4865$. The Hawk invasion barrier is $\tilde{\tilde{q}}_h = 0.9134$.

Figure 6 Initial conditions $q_h(0) = 0.89$ and $n(0) = 271/7$. Model parameters: $W = 1.6$, $d = 0.5$, $\Psi = 0.08$.

Figure 7 Initial conditions $q_h(0) = 0.89$ and $n(0) = 271/7$. Model parameters: $W = 7$, $d = 0.8$, $\Psi = 0.3$. 

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Fig. 1

Fig. 2
