

Non-Markov Stateful Evolutionary Games

Academic Editor: name

Version October 20, 2020 submitted to Games

Abstract: A new evolutionary game is introduced which incorporates states and actions into the strategies of the organisms of the evolving populations. The game centrally features actions that result in demographic flow between states that may not conserve organism numbers. It is by this feature that the game encapsulate a range of other evolutionary games, and can encode almost very complex interactions between organisms, species and populations. The game's formalism is expounded and the nature of the game's equilibrium is discussed. This discussion leads to an algorithm for numerically determining the stable equilibrium points which is exemplified in the context of a modified Hawk-Dove game. The game's flexibility for modeling population dynamics is evaluated and compared with other evolutionary games.

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Keywords: Evolutionary stable strategies (ESS); Markov decision evolutionary games (MDEG); Hawk-Dove game; Evolutionary dynamics; Evolutionary Game Theory

1. Introduction

Biological species are well recognised as being engaged in an evolutionary fight-for-survival and Game Theory has been used to analyse the strategies in such a fight. This kind of analysis is the defining feature of Evolutionary Game Theory, whose many features and concepts are often credited to John Maynard Smith and George R. Price [1, 2]. The most standard evolutionary game concerns the continuous growth/decay of organism types; the organism types are defined by the strategy they play as they are continuously randomly paired to participate in a simultaneous symmetric two-player game where the expected payoff determines each participant's growth [3]. However, there is sometimes felt to be a component missing from evolutionary analysis of strategies - the consideration of state [4].

Evolutionary game theory has been a valuable tool in characterising the dynamics and interactions among biological species and it also has proven utility in other fields which feature evolutionary dynamics. Some examples of phenomena which have been modeled via Evolutionary Game Theory include: altruism, empathy, human culture, moral behavior, private property, proto-linguistic behavior, social learning, societal norms, personality and mating-dynamics [5–7].

However, many organisms exhibit behaviors and strategies which are intrinsically coupled with state and hence cannot be directly modeled using standard evolutionary game theory. Simple and canonical examples include the behavior of perspiring with increasing body temperature causing dehydration, foraging behavior with hunger signals causing food shortage, sleep with ambient light levels causing vulnerability to predation, or hibernation with the change of season causing hunger.

Within this paper we detail an evolutionary game for modeling stateful evolutionary dynamics and an algorithm which solves for its equilibria. We give a simple demonstration of the game via an extension of the classic Hawk-Dove game [8] and we compare the game with the approach of others.

1.1. Related Work

Complex state-action interactions between individuals can always be stochastically modeled by artificial life simulations.[?]] But recent work has been conducted to incorporate some state-action dynamics into the exacting mathematical framework of evolutionary game theory.

This work has developed along two different branches, the first branch consists of encoding the organisms as belonging to nodes on a graph structure.[?]] In this approach the organisms at a node play the symmetric game against weighted probabilities of their nearest neighbors and/or themselves. Such games are called ‘Spatial Evolutionary Games’[? ?] and they have unique and dynamic behavior[? ?]. Spatial Evolutionary Games feature the addition of specifying a ‘who-plays-with-who’ into the game structure but the game itself is the same for all the participants. Spatial Evolutionary Games are apt to model the evolution of organism’s strategies between strategic nodes but it is seen to fail to capture the organisms having state beyond generalised location.

The second approach is more recent and consists of integrating state (and transitions between state) into the symmetric two-player game itself. This pioneering effort has centered around the works of Eitan Altman, and his colleagues Ilaria Brunetti and Yezekael Hayel [? ? ? ? ?], who introduce the Markov-Decision-Evolutionary-Game (MDEG) and variants thereof.

An MDEG consists in analysing the growth/decay of organism-types in a population where the organisms can occupy a finite set of states. The organism-types are defined by the strategy they play of choosing actions depending on their state as they are continuously randomly paired to participate in a two-player symmetric game. The game consists of each participant choosing an action and the game’s outcomes depend on the chosen actions and the states of the participants. The game’s outcomes determine the instantaneous payoff and probable transition to other states experienced by the participants. The expected long-term payoff determines the growth/decay of the organism-types which then changes the composition of the population in which the game is played.

Several example MDEG games are introduced in Altman’s literature including modifications and extensions of the Hawk-Dove game from which we take inspiration.[? ?] MDEG includes many features for modeling state-action interactions within evolutionary game theory and serves to provide a contrast for our game. By our game, we show that by relaxing the markov nature of MDEG we allow a remarkably more flexible game, a game which features other evolutionary games as subtypes.

1.2. Structure

The remainder of this paper is organised as follows: section ?? presents the core concept of non-markovian transmission of organisms between states, section ?? gives formalism to the non-markovian game and its algorithm, section ?? discusses the game’s equilibria and gives confinement for the algorithm’s equilibria search, section ?? details a Hawk-Dove game as example of the working algorithm, and section ?? concludes the paper by evaluating and comparing the features of our game.

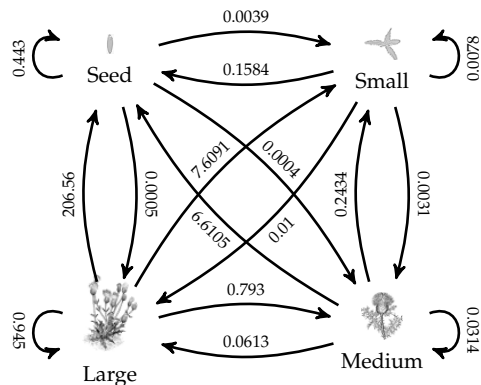
2. Non-Markov population models

The demographic flow of individuals of a species’ population between states is sometimes described in ecological-studies by a matrix that is not necessarily markov.[?]] The simplest example of such matrices are Leslie Matrices used for studying the structure of populations of individuals transitioning between evenly spaced age-states. Leslie Matrices are square, and they have form [?]:

$$M = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_{m-2} & F_{m-1} & F_m \\ P_0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & P_1 & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & P_2 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & P_{m-2} & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & P_{m-1} & 0 \end{bmatrix} \quad 0 < P_x < 1; F_x \geq 0$$

Where P_i represents the probability of an individual in the i th age bracket successfully living into the $(i + 1)$ th age bracket, and F_i is average number of offspring for an individual in i th age bracket within the duration of the age bracket. For a column vector $n = [n_0, n_1, n_2, \dots, n_m]$ with each n_i representing the number of individuals in each age-bracket, Mn gives the expected number of individuals in the population after the duration of one age bracket of time, and M^2n the expectation individuals after two age brackets, M^3n after three, and so on. Successive applications eventually yield a steady population profile between the n_i , and a constant exponential growth rate λ given by the Euler–Lotka equation. The λ is the dominant and only real-positive eigenvalue of the matrix, with the steady distribution n as its corresponding eigenvector, that is $Mn = \lambda n$.

Although the elements in the Leslie matrix are positive and represent states of organisms in the population and the transition between, the matrix isn't Markov because its columns don't necessarily sum to one. The informal difference is that whereas in a Markov-chain matrix the elements represent the expectation of *transition* between states, Leslie matrix elements represent the expectation of *transmission* between states inclusive of such possible factors as births and deaths. We term the class of such matrices as 'transmission matrices' in this article and assert the only thing defining such matrices are that they are real, square and have non-negative elements.¹ We do this because such matrices can be built more broadly than simple Leslie-matrix form[? ?]. Consider the rich interaction between organism-states captured by the matrix of transmissions for the 'Nodding Thistle' in figure ??.



(a) Life cycle graph of the population model

$$\begin{bmatrix} \text{Seed}_{t+1} \\ \text{Small}_{t+1} \\ \text{Medium}_{t+1} \\ \text{Large}_{t+1} \end{bmatrix} = \begin{bmatrix} 0.443 & 0.1584 & 6.6105 & 206.56 \\ 0.039 & 0.0078 & 0.2434 & 7.6091 \\ 0.0004 & 0.0031 & 0.0314 & 0.793 \\ 0.0005 & 0.01 & 0.0613 & 0.945 \end{bmatrix} \begin{bmatrix} \text{Seed}_t \\ \text{Small}_t \\ \text{Medium}_t \\ \text{Large}_t \end{bmatrix}$$

(b) 4x4 matrix model of a Nodding Thistle (*Carduus nutans*) population in Australia, classification based on seed and rosette size. The transmission numbers represent aggregate survival/growth/propagation of individuals from one class into another per year. The projected population growth rate (λ) is 1.207 per year. Data from Jongejans et.al[? ?]

Original data from Shea et.al[? ?]

Figure 1

It is by these transmission matrices that we are able to highlight the notion of transmission between two states as being the demographic flow of the population from one to the other. This notion forms a core concept in the next section as we introduce actions for the organisms and thence compare strategies in game-theory analysis for equilibria.

¹ General non-negative real square matrices (or at-least irreducible ones) have at-least one real non-negative eigenvalue (via indirect application of Perron-Frobenius theorem, see chapter 3 of [? ?]) hence a transmission matrix identifies at-least one growth-rate

3. Description of the Game

Consider an ecosystem of different species of organisms, where the organisms of each species have a distinct set of states which they can occupy. Further imagine that each state has a set of actions which an organism in the state can execute. Let:

- K be a finite set of species
- S be the finite set of all states
- S_k be nonempty disjoint subsets of states S available to species $k \in K$
- A be the finite set of all actions
- A_k be nonempty disjoint subsets of actions A available to species $k \in K$
- $A_{k,s}$ be nonempty subset of actions A_k available to species $k \in K$ in state $s \in S_k$

Further imagine that each individual organism has a strategy in addition to its state, which encodes the probabilities of what action it will execute depending on the state it is in. Let:

- W^k be the set of possible strategies for species $k \in K$, such that for any strategy $w^k \in W^k$ that $w_{a,s}^k$ denotes the probability that an organism with strategy w^k will execute action $a \in A_{k,s}$ if it is in state $s \in S_k$.

The elements of W^k are all that satisfy the basic rules of probability:

- probabilities of taking actions from any state must sum to one:

$$\forall k \in K \forall w^k \in W^k \forall s \in S_k \sum_{a \in A_{k,s}} w_{a,s}^k = 1$$

- all probabilities must be non-negative:

$$\forall k \in K \forall w^k \in W^k \forall s \in S_k \forall a \in A_{k,s} w_{a,s}^k \geq 0$$

- inaccessible actions have probability of zero:

$$\forall k \in K \forall w^k \in W^k \forall s \in S_k \forall a \notin A_{k,s} w_{a,s}^k = 0$$

The remaining elements are:

- $P_{t,k,s,w}$ is the number² of organisms at time t of species $k \in K$ in a state $s \in S^k$ with strategy $w \in W^k$;
- $P_{t,k,s,a}^* = \sum_{w^k \in W^k} P_{t,k,s,w} w_{a,s}^k$ is the number of organisms at time t of species $k \in K$ in a state $s \in S^k$ which are going to take action $a \in A_{k,s}$.
- $T_{k,s,a}(P_t^*)$ are positive functions of argument³ P_t^* , giving transmission of organisms (of a strategy w^k) to state $s \in S_k$ when action $a \in A_k$ is executed by an organism (of strategy w^k).
- α as the proportion of the population that will take an action at a time step $t \rightarrow t+1$; $0 < \alpha < 1$.

Once the above elements K, S, A, T, α and initial population P_0 are specified - the game's process is fully specified.

The game's process consists of stages: The organisms in the population of a strategy w^k have population distribution across states given by P_t . α of the those individuals have w^k strategy which determines the distribution of actions taken by them. The total actions taken by all strategies determines the total transmissions among the states - thus updating P_t to P_{t+1} . The process is embedded as Algorithm ??.

From Algorithm ?? is noticed that if the states were indexed $S_k = \{s_{k,0}, s_{k,1}, \dots\}$, that every strategy w^k would have its own transmission matrix analogous to those given in section ??:

$$m_{l,j} = M_{s_{k,l},s_{k,j}}^{t,k,w^k} = \sum_{a \in A_{k,s_j}} T_{k,s_{k,l},a}(P_t^*) w_{a,s_{k,j}}^k \quad (1)$$

² $P_{t,k,s,w}$ defines a distribution of the population at time t , which may be normalised and hence represent a probability distribution or left unnormalised as representing actual numbers of organisms. The only constraint is that it be non-negative $\forall t, k, s, w \ P_{t,k,s,w} \geq 0$. If the probability distribution is to be normalised then the normalisation can either be 'built-in' to the transmission T terms or included as a separate step in the algorithm ??

³ where P_t^* is shorthand for the set of all the numbers across k, s and a , $P_t^* = \{P_{t,k,s,a}^* \mid k \in K, s \in S_k, a \in A_{k,s}\}$

Algorithm 1 Forward Stepping Algorithm

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1: procedure SIMULATE( $K, S, W, T, P_0, \alpha, t_{max}$ )
2:    $t \leftarrow 0$ 
3:   while  $t < t_{max}$  do
4:      $P_{t,k,s,a}^* \leftarrow \sum_{w^k \in W^k} P_{t,k,s,w^k} w_{a,s}^k$  ▷ calculate reduced population distribution
5:     for  $k \in K$  do ▷ for each species:
6:       for  $w^k \in W^k$  do ▷ for each strategy:
7:          $M_{s_1,s_2}^{t,k,w^k} \leftarrow \sum_{a \in A_{k,s_2}} T_{k,s_1,a}(P_t^*) w_{a,s_2}^k$  ▷ calculate total transmissions
8:          $z_{s_1} \leftarrow \sum_{s \in S^k} M_{s_1,s}^{t,k,w^k} P_{t,k,s,w^k}$  ▷ apply matrix to the strategy's population
9:          $P_{t+1,k,s,w^k} \leftarrow \alpha z_s + (1 - \alpha) P_{t,k,s,w^k}$  ▷ incorporate new population by  $\alpha$ 
10:      end for
11:    end for
12:     $t \leftarrow t + 1$ 
13:  end while
14:  return  $P_{t_{max}}^*$ 
15: end procedure

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Such that $m_{l,j}$ would be net transmission from the j th state to the l th state for the individuals that take actions. We term such a matrix the "strategy's transmission matrix". Furthermore that if the actions were indexed $A_{k,s_{k,j}} = \{a_{k,j,0}, a_{k,j,1}, \dots\}$ that the probabilities of any strategy $w^k \in W^k$ would form an indexed set of numbers which we define to be the strategy's "terms".

$$q_{j,i} = w_{a_{k,j,i}, s_{k,j}}^k \quad (2)$$

Any appropriately dimensioned indexed set of numbers $q_{j,i}$ can be the terms of a strategy if it is "implementable". which is iff: $\forall j \sum_i q_{j,i} = 1$ and $\forall i, j q_{i,j} \in \mathbb{R}_+ \cup \{0\}$, ie. if the numbers could be taken to be probabilities of a strategy. The terms of a strategy are the same size and dimensions as all the strategies of the same species, and so it possible to add, subtract and multiply them together element-wise to form linear combinations of strategy terms. The result of a linear combination of strategy terms is implementable if the coefficients of the linear combination are positive and sum to unity. In the next section we will talk of linear combinations of strategies in this manner.

In anticipation of Appendix ?? we will present it here that: any strategy's transmission matrix has a form where it has columns are linear combination of column vectors weighted by its terms. Consider that if we index the T functions as $y_{j,i,l} = T_{k,s_{k,l}, a_{k,j,i}}$, and if $y_{j,i}$ denotes a column of such terms then $m_{l,j}$ has form:

$$m_{l,j} = \sum_i y_{j,i,l} q_{j,i} = \left[y_{0,0} q_{0,0} + y_{0,1} q_{0,1} + y_{0,2} q_{0,2} + \dots \mid y_{1,0} q_{1,0} + y_{1,1} q_{1,1} + \dots \mid y_{2,0} q_{2,0} + \dots \right] \quad (3)$$

4. Searching for Stable Equilibria

In direct correspondence with standard game theory language [?], it is possible to define basic relationships between the strategies. Each organism's strategy w^k encodes the probabilities of what actions it will take across its states. A strategy is 'pure' if these probabilities encode certainty of taking a single action per state otherwise it is 'mixed'. Any mixed strategy can be decomposed (perhaps not uniquely) into a linear combination of pure strategies. And any set of pure strategies defines a span

of mixed strategies which can be linearly composed of them. The set of pure strategies which could feature in a linear decomposition of a mixed strategy is defined as the ‘support’ of the mixed strategy.

If we define an ‘equilibrium’ as being the condition where all the $m_{i,j}$ transmission matrices remain constant - and an ‘equilibrium point’ being defined by those values. Then then it is necessarily the case that an equilibrium leads to a condition where all the species and strategies that are significantly present in the population are steadily growing by the same growth-rate in steady-state (see appendix ?? for discussion and a limited proof). For if any organisms of a strategy existed in the population with a lesser steady-state growth-rate then it would proportionally die out, or if any organisms of a strategy existed with a greater steady-state growth-rate then it would lead the others to proportionately die out.

We further define the equilibrium as being ‘stable’ in a similar way to Maynard Smith [? ? ?], specifically if it cannot be disturbed from equilibrium by the presence of a small incorporation-of (or ‘invaded by’) any possible ‘mutant’ strategy. We note that this is at-least the case where no ‘mutant’ strategy has a greater steady-state growth-rate in the context of the population.

It is proven in appendix ?? that for any stable equilibrium established with a population of mixed strategies that it is possible to establish the same equilibrium point without mixed strategies at all. Informally the reasoning is that: because any mixed strategy is a stochastic mix of its supporting pure strategies it can only perform as well as the best of them. And when it performs equal to the best then they must all perform equally. And in this case there is an equivalent combination of the supporting strategies which have the same state-action profile $P_{t,k,s,a}^*$ as as the mixed strategy; the same profile which defines the transmission matrices and thus the equilibrium point itself.

From these considerations it is thus unnecessary to consider mixed strategies in the search for stable equilibria because every stable equilibria can be established by combinations of pure strategies alone (although there may be zero or multiple such stable equilibria between them). In this way, multiple runs of Algorithm ?? with different initial combinations of pure strategies is sufficient to determine all possible stable equilibria of the game.

4.1. Software Implementation

An implementation of Algorithm ?? for arbitrary configuration of Species/States/Actions using pure strategies was written in the [Python](#) programming language using [Scoop](#) and [SymPy](#) libraries for parallelisation and for mathematical expression parsing respectively. The source-code is available at <https://github.com/Markopolo141/FSM-evolve/> and at the time of publication consists of a small and readable ~400 lines.

5. A Quick Example

One of the most famous evolutionary games is that of Hawk-Dove[?] which has been extended to multiple states by Eitan Altman et al[? ?]. A simplified version of Altman’s game (as presented in [?]) is as follows:

- $K = \{b\}$ A singular species of bird
- $S = S_b = \{y, a, p\}$ are the states of: young, aggressive adult, passive adult
- $A = A_b = \{R_a, R_p, G_a, G_p\}$, $A_{b,y} = \{G_a, G_p\}$, $A_{b,p} = \{R_p\}$, $A_{b,a} = \{R_a\}$ are actions available to various states: G_a/G_p is grow into aggressive/passive adult, R_a/R_p is reproduce aggressively/passively.

- All the transmission rates are:

$$\begin{array}{llll} T_{b,y,G_a}(P_t^*) = 0 & T_{b,y,G_p}(P_t^*) = 0 & T_{b,y,R_a}(P_t^*) = 2(1-p) & T_{b,y,R_p}(P_t^*) = 1-p+A \\ T_{b,a,G_a}(P_t^*) = 1-pC & T_{b,a,G_p}(P_t^*) = 0 & T_{b,a,R_a}(P_t^*) = 0 & T_{b,a,R_p}(P_t^*) = 0 \\ T_{b,p,G_a}(P_t^*) = DpC & T_{b,p,G_p}(P_t^*) = DpC + 1-pC & T_{b,p,R_a}(P_t^*) = 0 & T_{b,p,R_p}(P_t^*) = 0 \end{array}$$

where A, D, C are parameters of the game all between 0 and 1, and $p = \frac{P_{t,b,a,R_a}^*}{P_{t,b,a,R_a}^* + P_{t,b,p,R_p}^*}$

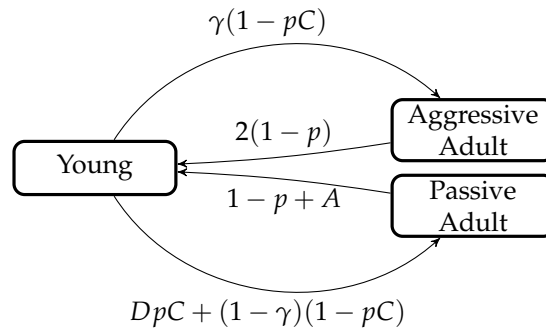


Figure 2. A diagram of the flow of individual organisms between states of a simple Hawk-Dove game γ being strategy parameter between G_a and G_b , p being proportion of Adults that are Aggressive, and A, D, C being game parameters

It is noted that the only state which has multiple actions available to it is y with G_a and G_p , and therefore the any strategy w^b is totally specified once $\gamma = w_{G_a, y}^b$ is specified, thus all strategies of the game can be parameterised by a single number γ , with $0 \leq \gamma \leq 1$.

If the states are indexed in order y, a, p and the actions are indexed in order R_a, R_p, G_a, G_p then a strategy w^b where $\gamma = w_{G_a, y}^b$ has transmission matrix $m_{i,j}$ of the form:

$$m_{i,j} = \begin{bmatrix} 0 & 2(1-p) & 1-p+A \\ \gamma(1-pC) & 0 & 0 \\ DpC + (1-\gamma)(1-pC) & 0 & 0 \end{bmatrix} \quad (4)$$

The demographic flow of organisms of strategy w^b between states can be visualised as per Figure ??.

We compared the results of the python software (of section ??) on the Hawk-Dove game with those obtained by mathematical analysis (as given in Appendix ??) and also via stochastic simulation.

The Moran process is a very simple stochastic model of the evolution of finite populations, wherein each 'turn' a random individual is chosen for reproduction proportional to its fitness and a corresponding random individual is chosen for death, the Moran process is generally regarded as a cornerstone technique of stochastic evolutionary game dynamics.[?]

A Moran process for the above game is programmed (with source-code shown in Appendix ??) and the results of the Moran process against the python implementation and mathematical analysis are shown in figure ??.

The figure shows the value p (the proportion of adults that are aggressive) and the proportion of young (%Y) at equilibrium against the parameter A for fixed C and D and shows a strong coincidence in achieving a non-trivial result for all three methodologies.

6. Discussion

The game (as defined in section ??) is designed with broad features to encapsulate a large number of potential applications. The game's elements consist of there being a population/s of entities that can be described as stateful and stochastically transmit themselves between states based on their present state and the states and actions of others in accordance with a conserved strategy of choosing actions.

It should be quite straightforward that the game's representation encapsulates other evolutionary games:

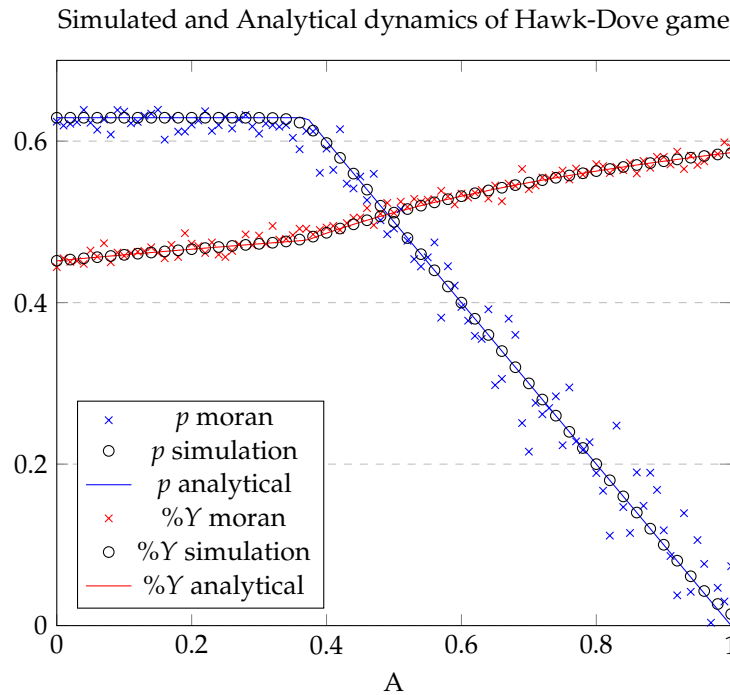


Figure 3. Dynamics of the Hawk-Dove game across parameter A , with $D = 0.75$ and $C = 0.70$ shown are results for p as well as proportion Young $\%Y$ for Moran stochastic simulation, analytical prediction, and our software solver's results

- **Classical evolutionary games** feature a finite set of strategies, each with growth-rates according to the expected payoff against the population of strategies. The rather degenerate analogue in our game, would have a single species with a single state and multiple actions of transmission to that same single state. Each of these actions would correspond to a strategy and would have transmission in proportion to its payoff.
- **Spatial evolutionary games** feature a finite set of strategies across nodes, each with growth-rates according to expected payoff against its neighbors. The analogue in our game, would consist in modeling each node as a separate species, each with a single state and multiple action of transmission to the single state. Each action would correspond to a strategy at a node and any action's transmission would be in proportion to its payoff against its neighbors.

Furthermore we observed (although not yet proven) that MDEG games are also encapsulated:

- **MDEG games** seem to be closely analogued in our game as having the exact same states and actions and almost having the same transmissions between states. In an MDEG game, the transmissions between states are conservative in the sense that playing an action never directly changes the net total number of individuals in the population but results in an additive payoff whos long-term value determines the growth-rate for the strategy. We have observed that the same dynamics can be encapsulated in our game by having the same conservative action transmissions plus a small multiple of the payoff values that would be achieved in the original MDEG game.

The breadth of our game's flexibility comes from allowing the transmission terms $T_{k,i,j}$ to be any function of population state P_t^* .

For instance, the T terms can be non-linear and represent non-linear dynamics between individuals, such as might be encoded in a classical evolutionary game with a 3-player symmetric payoff matrices. The T terms might keep the total population size under a maximum, or only under a maximum or

minimum for a particular state. They may encode dynamics similar to various evolutionary models eg. replicator dynamics, best-response dynamics or payoff comparison dynamics.[?]

In short, the game's T terms can encode significantly complex interactions between organisms, species and populations.

Consideration must be made in running the game's simulation (per algorithm ??) that there is no guarantee it will fall into a stable equilibrium, or that it will do so in a timely manner. This is particularly true if astability is intrinsically part of the model (such as the game of paper-scissors-rock [?]). It is also worth noting that setting α too high can potentially introduce astability into borderline stable models.

A limitation of our game is that it is intentionally designed to 'wash-out' periodic transients between the states as the simulation progresses (as $\alpha < 1$ acts as a dampener on such transients) so it cannot be used to model populations in which long-term periodic behavior between states in the simulation is desired⁴. Another limitation is that there is no current facilitation for transmission of organisms from one strategy into another, such as might be used to explicitly model the effects of significant mutation on the population (see Novak [?] for example analysis).

These limitations notwithstanding, hopefully it is seen that this article serves as a step towards the incorporation of state (in the most general sense) into evolutionary game theory analysis.

Acknowledgments:

Conflicts of Interest: The authors declare no conflict of interest. And the founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

Appendix A That all proportionally present strategies have the same growth-rate at equilibrium

At an equilibrium, if $m_{l,j}^{w^k}$ is the constant transmission matrix for strategy w^k , and if $v_j^{w^k,t} = P_{t,k,s_{k,j},w^k}$ is a vector of the number of organisms at time t of strategy w^k in the j th state. Then application of the transmission matrix to the vector gives the vector at the next time index $t + 1$ via Algorithm ?? as:

$$v_l^{w^k,t+1} = \alpha \left(\sum_j m_{l,j}^{w^k} v_j^{w^k,t} \right) + (1 - \alpha) v_l^{w^k,t+1} \quad \text{ie.} \quad v^{w^k,t+1} = (\alpha m^{w^k} + (1 - \alpha)I) v^{w^k,t}$$

Thus the strategy's population vector $v^{w^k,t}$ can be stepped forward in time by repeated matrix multiplication by the non-negative matrix $Z = (\alpha m^{w^k} + (1 - \alpha)I)$ where I is identity matrix.

It is generally observed that repeated matrix powers often yields exponential growth and if we assume Z is irreducible and diagonalisable matrix then the proof is straightforward and Theorem ?? gives the desired result:

$$\lim_{m \rightarrow \infty} \frac{v^{w^k,t}}{(\alpha \lambda_{w^k} + (1 - \alpha))^t} = b^{w^k} \hat{v}^{w^k} \quad \text{thus:} \quad v^{w^k,t} \approx (\alpha \lambda_{w^k} + (1 - \alpha))^t b^{w^k} \hat{v}^{w^k} \quad (5)$$

Where λ_{w^k} and \hat{v}^{w^k} are largest eigenvalue and corresponding eigenvector of m^{w^k} , and b^{w^k} is a constant. If we assume the same is true for all strategies in the population then each has an asymptotic exponential growth-rate $\gamma_{w^k} = \alpha \lambda_{w^k} + 1 - \alpha$. And so between any two strategies w^k and w^p , that if $\lambda_{w^k} > \lambda_{w^p}$ then $\gamma_{w^k} > \gamma_{w^p}$ and strategy w^k dominates strategy w^p . Thus between the strategies in the population the only strategies that will be ultimately undominated are those of the maximum growth-rate. And thus at equilibrium the only strategies of significant proportion in the

⁴ although α *could* be set to 1 to facilitate this

population have the same growth-rate γ .

The set of possible matrices m^{w^k} (and Z) is obviously much larger than those diagonalisable and irreducible. And while is generally observed that most matrices yield the same exponential-growth character there are some which don't, specifically defective matrices⁵. In this paper we assume such matrices are the rare exception and our analysis does not treat their case. Although we believe that all conclusions of the paper hold with their case included it will be left to future (and more mathematically involved) work to demonstrate such.

Appendix B That any stable equilibrium point can always be among pure strategies

In this section we will attempt to prove that any stable equilibrium point can be established among pure strategies alone. The total demonstration of this claim is formulated in matrix mathematics to avoid any possible vagueness as Theorem ???. But because of this, there is a step of interpretation needed between accepting the Theorem and understanding its connection and relevance to our game. It is this interpretation that we address in this section.

To make this connection we begin by coming to a definition of a strategy's being 'replaceable' by other strategies, if there exists a possible replacement of one's organisms for the others' in a population such as would not disturb the equilibrium point. Then we re-frame this condition in terms of matrices such as to directly relate to the theorems. The theorems are then shown to demonstrate that all mixed strategies are replaceable by sets of pure strategies, which demonstrates the claim of this appendix.

Appendix B.1 on 'replaceable' strategy

Suppose that there are two populations $P1$ and $P2$ consisting of the same set of strategies W^k except that $P2$ has an additional mixed strategy w^Σ . Suppose that both have the same values of $P1_{t,k,s,a}^* = P2_{t,k,s,a}^* = P_{t,k,s,a}^*$ ie. the same numbers of the organisms at time t , of species k , in states s taking actions a in the population (as per definition in section ??).

As P_t^* defines the transmission matrices of any strategies (via equation ??) then the strategies in both populations have the same transmission matrices. Therefore if $P1$ is in stable equilibrium then so to is $P2$ and they both have the same equilibrium point.

At a stable equilibrium each strategy w^k in the population has the same maximal exponential growth-rate of γ (as per equation ?? in Appendix ??) as:

$$P_{t,k,s_{k,j},w^k} = \gamma^t b^{w^k} \hat{v}_j^{w^k}$$

And per definition of P_t^* (in section ??):

$$P_{t,k,s_{k,j},a}^* = \sum_{w^k \in W^k} P_{t,k,s_{k,j},w^k} w_{a,s_{k,j}}^k = \gamma^t \sum_{w^k \in W^k} b^{w^k} \hat{v}_j^{w^k} w_{a,s_{k,j}}^k$$

where each b^{w^k} is interpreted as the relative 'amount' of strategy w^k (especially if \hat{v}^{w^k} is normalised), Thus:

$$P1_{t,k,s_{k,j},a}^* = P2_{t,k,s_{k,j},a}^* \quad \text{implies:} \quad \gamma^t \left(\sum_{w^k \in W^k} b^{w^k} \hat{v}_j^{w^k} w_{a,s_{k,j}}^k \right) = \gamma^t \left(c^{w^\Sigma} \hat{v}_j^{w^\Sigma} w_{a,s_{k,j}}^\Sigma + \sum_{w^k \in W^k} c^{w^k} \hat{v}_j^{w^k} w_{a,s_{k,j}}^k \right)$$

⁵ consider the linear growth of vector $\begin{bmatrix} 1 \\ 1 \end{bmatrix}$ by repeated multiplications of matrix $\begin{bmatrix} 1 & 1 \\ 0 & 1 \end{bmatrix}$

If we let $d^{w^k} = \frac{b^{w^k} - c^{w^k}}{c^{w^k}}$, then this implies:

$$\hat{v}_j^{w^\Sigma} w_{a,s_{k,j}}^\Sigma = \sum_{w^k \in W^k} d^{w^k} \hat{v}_j^{w^k} w_{a,s_{k,j}}^{w^k}$$

Thus if there exists positive ‘amounts’ d^{w^k} of strategies in the set $w^k \in W^k$ such that the above condition is true, then $P1$ and $P2$ will have identical equilibrium point. And indeed any ‘amount’ of strategy w^Σ can be exchanged one for the others while keeping equilibrium. This leads naturally to our informal definition:

Definition 1. A strategy in the population $w^\Sigma \in W^k$ of growth-rate γ is ‘replaceable at stable equilibrium’ by a set of other strategies W^k , if all strategies $w \in W^k$ have a growth-rate γ and there exists positive coefficients c_w such that:

$$\forall j, a \quad \hat{v}_j^{w^\Sigma} w_{a,s_{k,j}}^\Sigma = \sum_{w \in W^k} c_w \hat{v}_j^w w_{a,s_{k,j}}^w$$

With \hat{v}^w denoting an eigenvector corresponding to growth-rate γ of w ’s transmission matrix per Appendix ??.

Appendix B.2 ‘replaceable’ strategy terms

The span of strategy transmission matrices are defined by their columns as weighted sums of column vectors (see equation ??). Each set of weights are the subsets of the strategy’s terms, and suffer the constraints of their being non-negative and summing to unity. The pure strategies have terms which are entirely 0s and 1s and their matrices are the extreme poles of such a span.

The condition of replaceability (as per the above definition ??) is a relationship of eigenvectors \hat{v}^w between several transmission matrices and the same probabilities which define them $w_{a,s}$. And thus replaceability is actually a very specific relationship of the eigenvectors of sets of matrices who’s columns are weighted sums of column vectors and the weights themselves.

We conclude this Appendix by giving a definition of “replaceability”, as it applies to the terms of strategies in precise mathematical language. It in relation to this definition that Theorem ?? applies, to the conclusion that any strategy is replaceable by pure strategies.

Definition 2. A ‘strategy’s terms’ $q_{j,i}$ is a set of numbers indexed by j, i such that $\forall j \sum_i q_{j,i} = 1$ and $\forall j, i \ q_{j,i} \in \mathbb{R}_+ \cup \{0\}$

Definition 3. A ‘pure’ strategy’s terms is a strategy’s terms $q_{i,j}$ such that $\forall i, j \ q_{i,j} \in \{1, 0\}$

Definition 4. For sets of element-wise non-negative column vectors $y_{j,i}$, a ‘strategy terms’ $q_{j,i}$ is ‘replaceable at stable equilibrium’ by other strategy terms q_0, q_1, \dots iff there exists positive real coefficients c_0, c_1, \dots such that:

$$\lambda = \max_z \rho(m(z)) = \rho(m(q)) = \rho(m(q_0)) = \rho(m(q_1)) = \dots$$

$$\text{and } \forall i, j \quad V(m(q), \lambda)_{j,q_{j,i}} = c_0 V(m(q_0), \lambda)_{j,q_{0,j,i}} + c_1 V(m(q_1), \lambda)_{j,q_{1,j,i}} + \dots$$

Where $m(q)$ denotes the matrix $m(q)_{l,j} = \sum_i y_{j,i,l} q_{j,i} = \begin{bmatrix} y_{0,0} q_{0,0} + y_{0,1} q_{0,1} + \dots & y_{1,0} q_{1,0} + \dots & \dots \end{bmatrix}$

Where $\rho(\cdot)$ denotes spectral radius.

Where $\hat{V}(\cdot, \lambda)$ denotes an eigenvector of a matrix with an eigenvalue of magnitude λ

Appendix C The Proofs

Lemma 1. for sets of complex numbers λ_n and γ_n related by $\gamma_n = \alpha\lambda_n + 1 - \alpha$ for an α such that $0 < \alpha < 1$ and $\lambda_0 = \max_n(|\lambda_n|)$ that: $\gamma_0 = \max_n(|\gamma_n|)$ and for any $\gamma_m \neq \gamma_0$ that $|\gamma_m| < \gamma_0$

Proof. Applying the triangle inequality for any λ_m :

$$|\gamma_m| = |\alpha\lambda_m + 1 - \alpha| \leq |\alpha\lambda_m| + |1 - \alpha| = \alpha|\lambda_m| + 1 - \alpha$$

Therefore:

$$|\gamma_m| \leq \alpha \max_n(|\lambda_n|) + 1 - \alpha = \alpha\lambda_0 + 1 - \alpha = \gamma_0$$

Hence γ_0 is upper bound for set $|\gamma_m|$ and also is identical to an element in the set, hence is a maxima; satisfying the first part of the proof.

For a $\gamma_m \neq \gamma_0$ then $\lambda_m \neq \lambda_0$, and we break λ_m into real and imaginary components $\lambda_m = r_m + \mathbf{i}i_m$ (for \mathbf{i} being imaginary number).

If $r_m > \lambda_0$ then $\sqrt{r_m^2 + i_m^2} = |\lambda_m| > \lambda_0$ which is contradiction of construction of λ_0 .

If $r_m = \lambda_0$ then $\sqrt{r_m^2 + i_m^2} = |\lambda_m| \leq \lambda_0$ would only be true if $i_m = 0$, then $\gamma_m = \gamma_0$ contradicting construction of γ_m .

Therefore $r_m < \lambda_0$.

As $\gamma_m = \alpha\lambda_m + (1 - \alpha)$ then:

$$|\gamma_m|^2 = (\alpha r_m + (1 - \alpha))^2 + (\alpha i_m)^2 = \alpha^2(r_m^2 + i_m^2) + 2\alpha r_m(1 - \alpha) + (1 - \alpha)^2$$

Since $|\lambda_m| \leq \lambda_0$ therefore $r_m^2 + i_m^2 \leq \lambda_0^2$, and also that $r_m < \lambda_0$:

$$|\gamma_m|^2 < \alpha^2\lambda_0^2 + 2\alpha\lambda_0(1 - \alpha) + (1 - \alpha)^2 = (\alpha\lambda_0 + (1 - \alpha))^2 = |\gamma_0|^2$$

Therefore $|\gamma_m| < |\gamma_0|$, and the proof is complete. \square

Theorem 1. for an irreducible, diagonalisable non-negative real $n \times n$ matrix M with spectral radius λ , and non-negative non-zero vector v and an α such that $1 > \alpha > 0$, then for $Z = (\alpha M + (1 - \alpha)I)$.

That λ is an eigenvalue of M and its corresponding positive eigenvector z is such there is an $b \in \mathbb{R}_+$ that:

$$\lim_{m \rightarrow \infty} \frac{Z^m v}{(\alpha\lambda + (1 - \alpha))^m} = bz$$

Proof. Since M is irreducible and non-negative then it has a non-negative real eigenvalue λ_0 equal to its spectral radius λ and a corresponding positive eigenvector z_0 via Perron-Frobenius theorem. Let z_0, z_1, \dots and $\lambda_0, \lambda_1, \dots$ be set of complex eigenvectors/values for M (vectors as scaled to have magnitude of 1), in which case z_0, z_1, \dots and $\gamma_0, \gamma_1, \dots$ are eigenvectors/values for Z with $\gamma_i = \alpha\lambda_i + (1 - \alpha)$.

Since $\lambda_0 = \lambda$, then $\gamma_0 = \alpha\lambda_0 + (1 - \alpha)$ is unique largest magnitude eigenvalue of Z , as via lemma ??.

since z_0, z_1, \dots span \mathbb{C}^n , therefore v can be decomposed into a linear combination of them:

$$v = c_0 z_0 + c_1 z_1 + c_2 z_2 + \dots = \sum_i (v \cdot z_i) z_i \quad (\text{where } \cdot \text{ is hermitian inner product})$$

With c_0, c_1, \dots being the complex coefficients. Because vector v is non-negative and non-zero and z_0

is also positive therefore c_0 is real and positive. Taking m repeated applications of $\frac{1}{\gamma_0} Z$ gives:

$$\frac{Z^m v}{\gamma_0^m} = \left(\frac{\gamma_0}{\gamma_0}\right)^m c_0 z_0 + \left(\frac{\gamma_1}{\gamma_0}\right)^m c_1 z_1 + \left(\frac{\gamma_2}{\gamma_0}\right)^m c_2 z_2 + \dots$$

for large m , all terms with γ_{a_i} magnitudes less than that of γ_0 tend to zero leaving the single term:

$$\frac{Z^m v}{\gamma_0^m} = \left(\frac{\gamma_0}{\gamma_0}\right)^m c_0 z_0 = c_0 z_0$$

therefore:

$$\frac{Z^m v}{(\alpha\lambda_0 + (1 - \alpha))^m} = c_0 z_0$$

which completes the proof. \square

Lemma 2. for a $n \times n$ matrix A , and n column vector b , with $A^{b,k}$ denoting the matrix with its k th column as b . If λ is an eigenvalue for both A and $A^{b,k}$ then it is also an eigenvalue for $\alpha A + (1 - \alpha)A^{b,k}$ for any $\alpha \in \mathbb{R}$

Proof. Consider the characteristic polynomials of λ for A and $A^{b,k}$:

$$\det(A - \lambda I) = \det(A^{b,k} - \lambda I) = 0$$

If we let $C(\cdot)_{i,j}$ denote the i,j th cofactor of a matrix, then these determinants can be expanded along the k th column to give:

$$(\sum_i A_{i,k} C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = (\sum_i b_i C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = 0$$

Therefore:

$$\alpha ((\sum_i A_{i,k} C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k}) + (1 - \alpha) ((\sum_i b_i C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k}) = 0$$

$$= (\sum_i (\alpha A_{i,k} + (1 - \alpha) b_i) C(A - \lambda I)_{i,k}) - \lambda C(A - \lambda I)_{k,k} = \det(\alpha A + (1 - \alpha)A^{b,k} - \lambda I) = 0$$

Thus it is demonstrated that λ is also an eigenvalue for $\alpha A + (1 - \alpha)A^{b,k}$. \square

Theorem 2. For a real $n \times n$ element-wise non-negative matrix A , and real element-wise non-negative column vector b , with $A^{b,k}$ denoting the matrix with its k th column as b . For the matrix mapping $B(\alpha) = \alpha A + (1 - \alpha)A^{b,k}$ defined on a range $0 \leq \alpha \leq 1$. If $\rho(B(\alpha))$ denotes the spectral radius of $B(\alpha)$.

Then $\rho(B(\alpha))$ is continuous, and either constant or strictly monotonic with α .

Proof. Because $B(\alpha) = \alpha A + (1 - \alpha)A^{b,k}$ is a matrix continuous in all its elements it is thus well established that it will have n continuous eigenvalues[?].⁶

It is thus straightforward to note that the function $\rho(B(\alpha))$ is also continuous with α for all α .

Furthermore that the value $\rho(B(\alpha))$ is itself an eigenvalue of $B(\alpha)$ for all α via the Perron-Frobenius theorem. Suppose for a contradiction that $\rho(B(\alpha))$ is not monotone, in this case there must exist at least three values of α , $\alpha_1 < \alpha_2 < \alpha_3$ such that $\rho(B(\alpha_2)) > \max(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$ or $\rho(B(\alpha_2)) < \min(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$.

- suppose that $\rho(B(\alpha_2)) > \max(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$: let β be a value between $\rho(B(\alpha_2))$ and $\max(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$. Thus via the intermediate value theorem there exists γ_1 ($\alpha_1 < \gamma_1 < \alpha_2$) and γ_2 ($\alpha_2 < \gamma_2 < \alpha_3$) such that $\rho(B(\gamma_1)) = \rho(B(\gamma_2)) = \beta$. Thus β is an eigenvalue of $B(\alpha_1)$ (via Lemma ??), and $\beta > \rho(B(\alpha_1))$ which contradicts the construction of $\rho(B(\alpha_1))$.
- suppose that $\rho(B(\alpha_2)) < \min(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$: let β be a value between $\rho(B(\alpha_2))$ and $\min(\rho(B(\alpha_1)), \rho(B(\alpha_3)))$. Thus via the intermediate value theorem there exists γ_1 ($\alpha_1 < \gamma_1 < \alpha_2$) and γ_2 ($\alpha_2 < \gamma_2 < \alpha_3$) such that $\rho(B(\gamma_1)) = \rho(B(\gamma_2)) = \beta$. Thus β is an eigenvalue of $B(\alpha_2)$ (via Lemma ??), and $\beta > \rho(B(\alpha_2))$ which contradicts the construction of $\rho(B(\alpha_2))$.

Therefore $\rho(B(\alpha))$ is monotonic.

If there does not exist any $\alpha_1, \alpha_2 \in [0, 1]$ such that $\rho(B(\alpha_1)) = \rho(B(\alpha_2))$

then $\rho(B(\alpha))$ is strictly monotonic.

If there does exist an $\alpha_1, \alpha_2 \in [0, 1]$ such that $\rho(B(\alpha_1)) = \rho(B(\alpha_2))$

then $\rho(B(\alpha))$ is constant via lemma ??.

Which completes the proof. \square

⁶ An informal outline of the proof is that: 1. If the elements of a matrix are continuous 2. Then the coefficients of the characteristic polynomial are continuous (as they are additions and multiplications of them) 3. Then the roots of the characteristic polynomial are continuous (see [?]) 4. Hence the eigenvalues are continuous

Theorem 3. For a $n \times n$ matrix $A_{i,j}$, and column vectors b and c , with $A^{b,k}$ and $A^{c,k}$ denoting the matrix with its k th column as b and c respectively. For the matrix mapping $B(\alpha) = \alpha A^{b,k} + (1 - \alpha) A^{c,k}$ for $\alpha \in \mathbb{R}$. Let $\lambda(\alpha)$ and $v(\alpha)$ be an eigenvalue/vector pairing of $B(\alpha)$. If there exists different α_1 and α_2 such that $\lambda(\alpha_1) = \lambda(\alpha_2)$, then $\lambda(\alpha) = \lambda(\alpha_1)$ and $v(\alpha) = \frac{\alpha - \alpha_1}{\alpha_2 - \alpha_1} v(\alpha_2) + \frac{\alpha_2 - \alpha}{\alpha_2 - \alpha_1} v(\alpha_1)$ is a solution for all α , with $v(\alpha)_k$ being constant.

Proof. if $b = c$ then $A^{b,k} = A^{c,k}$ and $B(\alpha) = A^{b,k}$, then $\lambda(\alpha) = \lambda(\alpha_1)$ and $v(\alpha) = v(\alpha_1)$ is trivial solution which fulfills the proof. Otherwise $b \neq c$.

Since $\lambda(\alpha_1)$ is an eigenvalue for all $B(\alpha)$ via Lemma ?? then $\frac{\partial \lambda(\alpha)}{\partial \alpha} = 0$ and $\lambda(\alpha) = \lambda(\alpha_1) = \lambda$ is true.

As: $(\alpha A^{b,k} + (1 - \alpha) A^{c,k}) v(\alpha) = \lambda v(\alpha)$

If $v(\alpha)_k$ denotes the k th value of $v(\alpha)$, then differentiating with respect to α

Gives: $(\alpha A^{b,k} + (1 - \alpha) A^{c,k} - \lambda I) \frac{\partial v(\alpha)}{\partial \alpha} + (b - c) v(\alpha)_k = 0$

now, there are two cases:

if there is an α_3 such that $v(\alpha_3)_k = 0$ then:

$$(\alpha_3 A^{b,k} + (1 - \alpha_3) A^{c,k} - \lambda I) \frac{\partial v(\alpha_3)}{\partial \alpha} = 0$$

Setting $\frac{\partial v(\alpha)}{\partial \alpha} = 0$ is permissible, making $v(\alpha)_k = 0$.

therefore constant $v(\alpha) = v(\alpha_3)$ is solution which fulfills the proof

if there is not an α_3 such that $v(\alpha_3)_k = 0$, then:

It is possible to do scaling, thus setting $v(\alpha)_k = d$ to be a non-zero constant and therefore $\frac{\partial v(\alpha)_k}{\partial \alpha} = 0$

Thus there is a $\frac{\partial v(\alpha)}{\partial \alpha}$ such that: $(\alpha A^{b,k} + (1 - \alpha) A^{c,k} - \lambda I) \frac{\partial v(\alpha)}{\partial \alpha} + d(b - c) = 0$

Thus there is a $\frac{\partial v(\alpha)}{\partial \alpha}$ such that for all i : $(\sum_{j \neq k} (A_{i,j} - \lambda I_{i,j}) \frac{\partial v(\alpha)_j}{\partial \alpha}) + d(b_i - c_i) = 0$

Therefore $\frac{\partial v(\alpha)}{\partial \alpha}$ can be constant

Therefore $v(\alpha) = \frac{\alpha - \alpha_1}{\alpha_2 - \alpha_1} v(\alpha_2) + \frac{\alpha_2 - \alpha}{\alpha_2 - \alpha_1} v(\alpha_1)$ is only linear solution that adjoins $v(\alpha_2)$ and $v(\alpha_1)$.

Which completes the proof. \square

Theorem 4. For a real $n \times n$ element-wise non-negative matrix A , for m element-wise non-negative column vectors b_0, b_1, \dots , for $A^{b_i,k}$ denoting the matrix with its k th column as b_i , for the matrix mapping $B(c_0, c_1, \dots) = \sum_i c_i A^{b_i,k}$ defined on inputs where: $\forall_i c_i \geq 0$ and $(\sum_{i=0}^{m-1} c_i) = 1$, for $\rho(B)$ denoting the spectral radius of B , for $V(\cdot, \lambda)_k$ denotes the k th element of an eigenvector of a matrix corresponding to eigenvalue λ , for a set of reals d_0, d_1, \dots :

If: $\rho(B(d_0, d_1, \dots)) = \max \rho(B) = \lambda$ then:

$$V(B(d_0, d_1, \dots), \lambda) = \sum_{i=0}^{m-1} d_i V(A^{b_i,k}, \lambda) \quad \text{and:}$$

$\forall d_i \neq 0 \quad V(A^{b_i,k}, \lambda)_k = V(B(d_0, d_1, \dots), \lambda)_k = C$ ie. they all have the same k th value, equal C

Proof. We begin by introducing the following mapping on the coordinates c_0, c_1, \dots, c_{m-1} by parameter α , valid for $0 \leq \alpha \leq 1$ and $c_{m-1} \neq 1$:

$$Q(c_0, c_1, \dots, c_{m-1}, \alpha) = B\left(\frac{c_0(1-\alpha)}{\sum_{y=0}^{m-2} c_y}, \frac{c_1(1-\alpha)}{\sum_{y=0}^{m-2} c_y}, \dots, \frac{c_{m-2}(1-\alpha)}{\sum_{y=0}^{m-2} c_y}, \alpha\right) = \alpha A^{b_{m-1},k} + (1 - \alpha) \frac{\sum_{y=0}^{m-2} c_y A^{b_y,k}}{\sum_{y=0}^{m-2} c_y} \quad (6)$$

Q is a valid mapping under the input constraints, ie. that the inputs to B satisfy the constraints if the c -inputs of Q (the c_0, c_1, \dots, c_{m-1}) satisfy the constraints (that they are non-negative and they sum to one). We also notice by inspection of equation ?? that $Q(\dots, \alpha)$ satisfies the criteria for Theorem ?? and thus $\rho(Q(\dots, \alpha))$ is either constant or strictly monotonic. When $\alpha = 1$ the input to B takes the singular value: $Q(c_0, c_1, \dots, c_{m-1}, 1) = B(0, 0, \dots, 1) = A^{b_{m-1},k}$ (7)

When $\alpha = 0$ the input to B takes the zero of the last value with the other values scaled to validate input constraints:

$$Q(c_0, \dots, c_{m-1}, 0) = B(\gamma c_0, \dots, \gamma c_{m-2}, 0) = B(\gamma c_0, \dots, \gamma c_{m-2}) \quad \text{with: } \gamma = (\sum_{i=0}^{m-2} c_i)^{-1} \quad (8)$$

$$\text{And when } \alpha = c_{m-1} \text{ that } Q(c_0, c_1, \dots, c_{m-1}, c_{m-1}) = B(c_0, c_1, \dots, c_{m-1}) \quad (9)$$

Proof by induction:

- Considering the case $m = 1$: In which case there is a singular vector b_0 and the only permissable value of $B(d_0)$ under the constraints is $B(1)$ therefore $V(B(d_0), \lambda) = V(A^{b_0, k}, \lambda)$ thus the theorem is satisfied for $m = 1$.

- Considering the case $m = j + 1$ under the assumption of theorem satisfaction of $m = j$:

If $d_j = 1$ then:

$$V(B(d_0, d_1, \dots), \lambda) = V(A^{b_j, k}, \lambda) \text{ and the theorem is satisfied}$$

Otherwise:

$\rho(Q(d_0, d_1, \dots, d_j, \alpha))$ exists and is constant or strictly monotonic with α

- as per theorem ?? on equation ??

$$\rho(Q(d_0, d_1, \dots, d_j, \alpha)) \text{ passes through } \rho(B(d_0, d_1, \dots, d_j))$$

- as per equation ??.

$$\text{Assuming } \rho(B(d_0, d_1, \dots, d_j)) \geq \max(\rho(Q(c_0, c_1, \dots, c_j, 1)), \rho(Q(c_0, c_1, \dots, c_j, 0)))$$

- which is a condition of the theorem.

Therefore there are three cases:

$$\text{If } d_j = 1 \text{ then } \rho(B(d_0, d_1, \dots, d_j)) = \rho(Q(c_0, c_1, \dots, c_j, 1)):$$

$$\text{Then } V(B(d_0, d_1, \dots), \lambda) = V(A^{b_j, k}, \lambda) \text{ and the theorem is satisfied}$$

$$\text{If } d_j = 0 \text{ then } \rho(B(d_0, d_1, \dots, d_j)) = \rho(Q(c_0, c_1, \dots, c_j, 0)):$$

$$\text{Then } B(d_0, d_1, \dots, d_{j-1}, d_j) = B(d_0, d_1, \dots, d_{j-1})$$

$$\text{And } V(B(d_0, d_1, \dots, d_{j-1}, d_j), \lambda) = V(B(d_0, d_1, \dots, d_{j-1}), \lambda)$$

$$\text{And } V(B(d_0, d_1, \dots, d_{j-1}), \lambda) = \sum_{i=0}^{m-2} d_i V(A^{b_i, k}, \lambda)$$

- by the inductive assumption

$$\text{Thus } V(B(d_0, d_1, \dots, d_{j-1}, d_j), \lambda) = \sum_{i=0}^{m-1} d_i V(A^{b_i, k}, \lambda) \text{ and the theorem is satisfied}$$

Otherwise $\rho(Q(d_0, d_1, \dots, d_j, \alpha))$ must be constant with change in α :

Since $Q(d_0, d_1, \dots, d_j, \alpha)$ is non-negative matrix

Then $\rho(Q(d_0, d_1, \dots, d_j, \alpha)) = \lambda$ is an eigenvalue of it

-via the Perron-Frobenius theorem

$$\text{Thus via Theorem ??: } V(Q(d_0, d_1, \dots, d_j, \alpha), \lambda)$$

$$= \alpha V(Q(d_0, d_1, \dots, d_j, 1), \lambda) + (1 - \alpha) V(Q(d_0, d_1, \dots, d_j, 0), \lambda)$$

$$\text{and } V(Q(d_0, d_1, \dots, d_j, \alpha), \lambda)_k = C \text{ is constant irrespective of } \alpha$$

$$\text{So via equations ??, ??, ??: } V(B(d_0, d_1, \dots, d_j), \lambda)$$

$$= d_j V(A^{b_j, k}, \lambda) + (1 - d_j) V(B(\gamma d_0, \gamma d_1, \dots, \gamma d_{j-1}), \lambda) \quad \text{with: } \gamma = (\sum_{i=0}^{j-1} d_i)^{-1}$$

$$\text{And } V(B(d_0, d_1, \dots, d_j), \lambda)_k = V(A^{b_j, k}, \lambda)_k = V(B(\gamma d_0, \gamma d_1, \dots, \gamma d_{j-1}), \lambda)_k = C$$

$$\text{As } V(B(\gamma d_0, \gamma d_1, \dots, \gamma d_{j-1}), \lambda) = \gamma \sum_{i=0}^{m-2} d_i V(A^{b_i, k}, \lambda)$$

- by the inductive assumption

$$\text{and each non-zero } d_i \text{ has } V(A^{b_i, k}, \lambda)_k = C$$

$$\text{Thus: } V(B(d_0, d_1, \dots, d_j), \lambda) = \sum_{i=0}^{m-1} d_i V(A^{b_i, k}, \lambda) \text{ and the theorem is satisfied}$$

Which completes the proof. \square

Theorem 5. For n sets of real element-wise non-negative n -column vectors, $\{y_{0,0}, y_{0,1}, \dots, y_{1,0}, y_{1,1}, \dots\}$.

Letting q be similarly dimensioned set of sets of real numbers, $q = \{q_{0,0}, q_{0,1}, \dots, q_{1,0}, q_{1,1}, \dots\}$

Letting $q^{\{i,j\}}$ be the same as q except modified in that the subset q_i is all zeros except for the j th being 1.

Letting $q^{\{i,j\},a,b,c,\dots}$ be the same as $q^{\{i,j\}}$ except that the first unmodified subset is all zeros except for the a th being 1, and the second unmodified q subset is all zeros except for the b th, and etc.

Considering matrix constructions of form:

$$m(a) = \left[\begin{array}{c|c|c|c} \sum_x a_{0,x} y_{0,x} & \sum_x a_{1,x} y_{1,x} & \sum_x a_{2,x} y_{2,x} & \dots \end{array} \right]$$

Defined for any a input such that: $\forall j \sum_i a_{j,i} = 1$ and $\forall j, i \ a_{j,i} \geq 0$.

for $\rho(\cdot)$ is spectral radius, and $V(\cdot, \lambda)$ is an eigenvector of a matrix for eigenvalue λ , and δ is Kronecker delta.

If $\rho(m(q)) = \max_{\zeta} \rho(m(\zeta)) = \lambda$

Then

$$\forall i, j \ V(m(q), \lambda)_{j,i} = \sum_k \sum_{\alpha} \dots \sum_{\omega} q_{0,\alpha} \dots q_{n-1,\omega} V(m(q^{\{j,k\},\alpha,\beta,\gamma,\dots,\omega}), \lambda)_{j,i} \delta_{ik}$$

Proof.

For any j , Theorem ?? applies to $m(q)$ on the j th set of q 's values:

Therefore $V(m(q), \lambda) = \sum_i q_{j,i} V(m(q^{\{j,i\}}), \lambda)$ and $\forall i \ V(m(q^{\{j,i\}}), \lambda)_{j,i} = C$ is a constant.

Thus $V(m(q), \lambda)_j = \sum_i q_{j,i} V(m(q^{\{j,i\}}), \lambda)_j = \sum_i q_{j,i} C = C$, and

Therefore $\forall i \ V(m(q), \lambda)_j = V(m(q^{\{j,i\}}), \lambda)_j$

Thus $\forall i \ q_{j,i} V(m(q), \lambda)_j = q_{j,i} V(m(q^{\{j,i\}}), \lambda)_j$

Thus $\forall i \ q_{j,i} V(m(q), \lambda)_j = \sum_k \delta_{ik} q_{j,k} V(m(q^{\{j,k\}}), \lambda)_j$ (10)

Now, theorem ?? applies to $V(m(q^{\{j,k\}}), \lambda)$:

therefore $V(m(q^{\{j,k\}}), \lambda) = \sum_{\alpha} q_{0,\alpha} V(m(q^{\{j,k\},\alpha}), \lambda)$

theorem ?? applies again to $V(m(q^{\{j,k\},\alpha}), \lambda)$:

therefore $V(m(q^{\{j,k\},\alpha}), \lambda) = \sum_{\beta} q_{1,\beta} V(m(q^{\{j,k\},\alpha,\beta}), \lambda)$

theorem ?? applies again to $V(m(q^{\{j,k\},\alpha,\beta}), \lambda)$:

therefore $V(m(q^{\{j,k\},\alpha,\beta}), \lambda) = \sum_{\gamma} q_{2,\gamma} V(m(q^{\{j,k\},\alpha,\beta,\gamma}), \lambda)$

and so on...

Therefore: $V(m(q^{\{j,k\}}), \lambda) = \sum_{\alpha} \sum_{\beta} \sum_{\gamma} \dots \sum_{\omega} q_{0,\alpha} q_{1,\beta} q_{2,\gamma} \dots q_{n-1,\omega} V(m(q^{\{j,k\},\alpha,\beta,\gamma,\dots,\omega}), \lambda)$ (11)

Which is fully expanded.

Substituting equation ?? into equation ?? gives:

$$\forall i \ q_{j,i} V(m(q), \lambda)_j = \sum_{\alpha} \sum_{\beta} \sum_{\gamma} \dots \sum_k \dots \sum_{\omega} q_{0,\alpha} q_{1,\beta} q_{2,\gamma} \dots q_{j,k} \dots q_{n-1,\omega} \delta_{ik} V(m(q^{\{j,k\},\alpha,\beta,\gamma,\dots,\omega}), \lambda)_j$$

Which completes the proof \square

478 Appendix D Derivation of Hawk-Dove dynamics

The Hawk-Dove game given in the body of the article is simple enough to yield analytic solution. It is possible to directly determine the largest real eigenvalue of the transmission matrix (as per equation ??) as:

$$\lambda = \sqrt{2\gamma(1-p)(1-pC) + (1-p+A)(DpC + (1-\gamma)(1-pC))}$$

479 And by this, it is posible to compute the equilibrium points of the population. The population's
480 equilibrium points will either be on the 'interior' of the strategy space ($1 > \gamma > 0$) or be on the
481 boundary ($\gamma = 1$ or $\gamma = 0$). We can calculate the interior equilibrium points via the 'indifference
482 principle'[?], whereby the population has reached an 'interior' equilibrium where it makes no more
483 sense to play Dove any more than Hawk. This corresponds to the case where all Dove and Hawk
484 strategies have the same growth-rate.

485 *Appendix D.1 the interior case for $1 > \gamma > 0$*

Solving for $\frac{\partial \lambda}{\partial \gamma} = 0$ gives

$$1 - p = A$$

As the conditions for interior equilibrium. This condition which corresponds to the Aggressive and Passive Adults having the same expected number of offspring. Thus the expected population growth-rate at equilibrium is thus

$$\lambda_{\{p=1-A\}} = \sqrt{2A} \sqrt{C(1-A)(D-1) + 1}$$

486 This identifies that the total growth-rate is the multiplication of the roots of transmission rate from
487 young to adult and from adult to young.

488 Using the shorthand: $P_Y = P_{t,b,y,G_a}^* + P_{t,b,y,G_p}^*$, and $P_A = P_{t,b,a,R_a}^*$, and $P_P = P_{t,b,p,R_p}^*$
489 The corresponding eigenvector of population proportions is (presented unnormalised for simplicity)
490 as:

$$\begin{bmatrix} P_Y \\ P_A \\ P_P \end{bmatrix} = \begin{bmatrix} \lambda_{\{p=1-A\}} \\ \gamma(1-C+CA) \\ DC(1-A) + (1-\gamma)(1-C+CA) \end{bmatrix}$$

491 Thus the fraction of Child to Adults at equilibrium is $\frac{P_Y}{P_Y+P_A+P_P} = \frac{\sqrt{2A}}{\sqrt{2A} + \sqrt{C(1-A)(D-1)+1}}$

492 *Appendix D.2 the boundary case for $\gamma = 1$*

The growth-rate of strategy $\gamma = 1$ is $\lambda_{\{\gamma=1\}} = \sqrt{2(1-p)(1-pC) + DpC(1-p+A)}$ and has population proportions:

$$\begin{bmatrix} P_Y \\ P_A \\ P_P \end{bmatrix} = \begin{bmatrix} \lambda_{\{\gamma=1\}} \\ 1-pC \\ DpC \end{bmatrix}$$

A population of $\gamma = 1$ (in which $p = \frac{P_A}{P_A+P_P}$) has $p = \frac{-(C+1) + \sqrt{(C+1)^2 + 4(DC-C)}}{2(DC-C)}$ (which exists if $(C+1)^2 + 4(DC-C) > 0$). The strategy $\gamma = 1$ is strictly dominant strategy when all other strategies have a lower growth-rate:

$$\forall \gamma \quad \lambda_{\{\gamma=1, p=\dots\}}^2 > \lambda_{\{p=\dots\}}^2$$

$$\forall \gamma \quad 2(1-p)(1-pC) + (1-p+A)DpC > 2\gamma(1-p)(1-pC) + (1-p+A)(DpC + (1-\gamma)(1-pC))$$

$$\forall \gamma \quad 1-p-A > \gamma(1-p-A)$$

which is true iff $p < 1 - A$, which thus happens on a condition among the A, C, D :

$$\sqrt{(C+1)^2 + 4(DC - D)} > 2(1 - A)(DC - D) + C + 1$$

When this condition is met, the strategy $\gamma = 1$ dominates, yielding $p = \frac{-(C+1) + \sqrt{(C+1)^2 + 4(DC - C)}}{2(DC - C)}$

with the fraction of Child to Adults $\frac{P_Y}{P_Y + P_A + P_P} = \frac{\sqrt{DpC(1+p+A)}}{\sqrt{DpC(1+p+A)} + 1 - pC + DpC}$

Appendix D.3 the boundary case for $\gamma = 0$

The growth-rate of strategy $\gamma = 0$ is $\lambda_{\{\gamma=0\}} = \sqrt{(1-p-A)(DpC + 1 - pC)}$ and has population proportions:

$$\begin{bmatrix} P_Y \\ P_A \\ P_P \end{bmatrix} = \begin{bmatrix} \lambda_{\{\gamma=0\}} \\ 0 \\ DpC + 1 - pC \end{bmatrix}$$

A population of $\gamma = 0$ (in which $p = \frac{P_A}{P_A + P_P}$) has straightforwardly $p = 0$ and growth-rate $\lambda_{\{\gamma=0, p=0\}} = \sqrt{1 - A}$.

However, in such a population the strategy $\gamma = 1$ has a greater growth-rate than $\gamma = 0$ as: $(\lambda_{\{\gamma=1, p=0\}} = \sqrt{2}) > (\sqrt{1 - A} = \lambda_{\{\gamma=0, p=0\}})$ and thus the boundary case $\gamma = 0$ is never an dominant strategy.

Appendix D.4 Stitching it together

Given the parameters of the game A, C, D is:

$$(C+1)^2 + 4(DC - D) > 0 \quad \text{and} \quad \sqrt{(C+1)^2 + 4(DC - D)} > 2(1 - A)(DC - D) + C + 1 \quad ?$$

- if so then the Game equilibrium is Hawk-Saturated:

$$p = \frac{-(C+1) + \sqrt{(C+1)^2 + 4(DC - C)}}{2(DC - C)} \quad \text{and} \quad \frac{P_Y}{P_Y + P_A + P_P} = \frac{\sqrt{DpC(1+p+A)}}{\sqrt{DpC(1+p+A)} + 1 - pC + DpC}$$

- if not then a Hawk-Dove equilibrium exists:

$$p = 1 - A \quad \text{and} \quad \frac{P_Y}{P_Y + P_A + P_P} = \frac{\sqrt{2A}}{\sqrt{2A} + \sqrt{C(1-A)(D-1)} + 1}$$

Appendix E Example Python source-code for Moran Process simulation

```

import random

num_bots = 1200
turns = num_bots*100
D = 0.75
A = 0.8
C = 0.70

bots = [(i%3,i%2) for i in range(num_bots)]

def add_bots(number, state, gamma):
    for i in range(int(number)):
        bots[random.randint(0, num_bots-1)] = (state, gamma)
    if random.random() < number-int(number):
        bots[random.randint(0, num_bots-1)] = (state, gamma)

def calculate_p():
    ah = 0
    ad = 0
    for b in bots:
        if b[0]==0:
            ah += 1
        if b[0]==1:
            ad += 1
    if ah+ad==0:
        return 0.0
    else:
        return (1.0*ah)/(ad+ah)

def turn(b):
    p = calculate_p()
    if b[0]==0:
        add_bots(2*(1-p), 2, b[1])
    if b[0]==1:
        add_bots(1-p+A, 2, b[1])
    if b[0]==2 and b[1]==0:
        add_bots(1-p*C, 0, b[1])
        add_bots(D*p*C, 1, b[1])
    if b[0]==2 and b[1]==1:
        add_bots(C*p*(D-1)+1, 1, b[1])

for i in range(turns):
    turn(random.choice(bots))
    if i%(turns/1000)==0:
        add_bots(1, random.randint(0, 2), random.randint(0, 1))
print "p_={} ".format(calculate_p())
print "proportion_Child_={} ".format(sum(
    [b[0]==2 for b in bots])*1.0 / num_bots)

```

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