# INDIVIDUAL BEHAVIOR IN AN STRUCTURED POPULATION: REDUCTION OF A DISCRETE SYSTEM COUPLING HAWK-DOVE TACTICS AND DEMOGRAPHY

M. Marvá*, R. Bravo de la Parra*
Dpto Matemáticas*, Dpto Ecología‡
Universidad de Alcalá. 28871 Madrid, Spain
marcos.marva@uah.es, rafael.bravo@uah.es

P. Auger†, M.A. Zavala‡
UR GEODES, IRD 32,†
Avenue Henri Varagnat, 93143 -Bondy cedex, France
Pierre.Auger@bondy.ird.fr, madezavala@gmail.com

## Aggregation techniques.

We consider a nonlinear discrete model including two processes evolving at different time scales: *slow* and *fast*. We assume that fast dynamics let constant some global variables and reach some equilibria for the state variables which depend on the global ones. In this case the asymptotic dynamics of the model can be studied through a reduced, *aggregated*, system for the global variables. [1].

We present a model of an age-structured population: juveniles ($n_1$) and adults ($n_2$). When competing for resources adults can be aggressive or passive. Behavior changes are assumed to be faster than demography.

## Hawk-dove tactics.

Confrontations between aggressive (hawk, $n_H$) and passive (dove, $n_D$) adults may entails costs ($C$) and gains ($G$). Adults are supposed to have the ability of switching their behavior according to their previous experiences. We represent behavior changes by means of the following discrete version of replicator equations associated to the classical hawk-dove game:

$$\begin{cases} n_1(t+1) = n_1(t), \\ n_H(t+1) = \dfrac{-(G+C)n_H^2(t)n_2(t) + (2G+C)n_H(t)n_2^2(t)}{-Cn_H^2(t) + (G+C)n_2^2(t)}, \\ n_D(t+1) = \dfrac{Gn_D^2(t)n_2(t) + Cn_D(t)n_2^2(t)}{-Cn_H^2(t) + (G+C)n_2^2(t)}. \end{cases} \qquad (1)$$

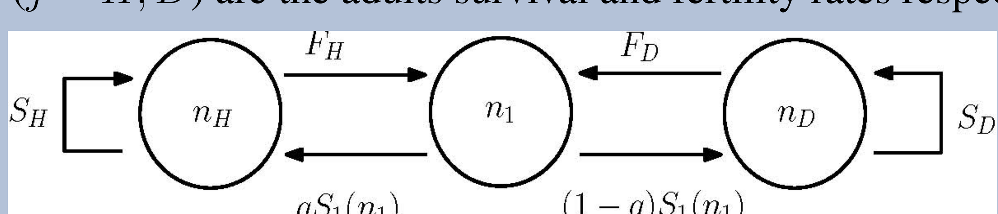
We denote the vector of state variables $n = (n_1, n_H, n_D)$ and the map $\mathcal{F}$ associated to system (1). The juvenile density, $n_1$, and the global adult density, $n_2 = n_H + n_D$, are kept constant through behaviour changes.

## Leslie type demography.

The demographic process is defined by means of the following matrix

$$\mathcal{L}(n_1(t)) = \begin{pmatrix} 0 & F_H & F_D \\ qS_1(n_1(t)) & S_H & 0 \\ (1-q)S_1(n_1(t)) & 0 & S_H \end{pmatrix} \qquad (2)$$

Where $S_1(n_1(t))$ is the juvenile survival rate which depends on juvenile density, $q$ is the fraction of juveniles becoming aggressive adults and $S_j$ and $F_j$ $(j = H, D)$ are the adults survival and fertility rates respectively.




## The complete system.

Competitive encounters, and subsequent changes of behavior, are more frequent that their reproductive counterparts. We represent it assuming a ratio k between characteristic time scales associated to behavior and demographic changes. which yield the **complete system**

$$\mathbf{n}(t+1) = \mathcal{L}(n_1(t)) \cdot \mathcal{F}^k(\mathbf{n}(t)), \qquad t = 1, 2, 3, \cdots \qquad (3)$$

The time unit of system (3) is the slow one and so we assume that fast dynamics act $k$ times along it by including the $k$-fold iterate of map $\mathcal{F}$.

**Proposition 1** (Fast equilibria) *Let $\mathcal{F}$ be the map to the fast dynamics and $\mathbf{n} = (n_1, n_H, n_D)$ any non-negative vector. Then, there exist constants $n_H^*$ and $n_D^*$ such that*

$$\lim_{k\to\infty} \mathcal{F}^k(\mathbf{n}) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & n_H^* & n_H^* \\ 0 & n_D^* & n_D^* \end{pmatrix} \begin{pmatrix} n_1 \\ n_H \\ n_D \end{pmatrix} = \bar{\mathcal{F}}(\mathbf{n})$$

$$\bar{\mathcal{F}}(\mathbf{n}) = \begin{pmatrix} 1 & 0 \\ 0 & n_H^* \\ 0 & n_D^* \end{pmatrix} \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} \begin{pmatrix} n_1 \\ n_H \\ n_D \end{pmatrix} = \mathcal{E} \cdot \mathcal{G} \cdot \mathbf{n} \qquad (4)$$

*where $(n_H^*, n_D^*) = (1, 0)$ **(pure hawk equilibrium)** if $G > C$ and $(n_H^*, n_D^*) = (G/C, 1 - G/C)$ **(polymorphic hawk-dove equilibrium)** if $G < C$. The limit (4) is $\mathcal{C}^1$-uniform on compact sets in the positive cone.*

The general results achieved in [1] allow us to study the general system through the **auxiliary system**

$$\mathbf{n}(t+1) = \mathcal{L}(n_1(t)) \cdot \bar{\mathcal{F}}(\mathbf{n}(t)), \qquad t = 1, 2, 3, \cdots \qquad (5)$$

Thanks to the limit (4) this approximation is equivalent to the assumption that the ratio between the fast and the slow time scales is infinity.

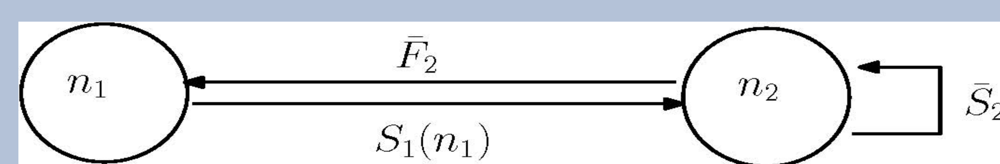
## The aggregated system.

Decomposition (4) is key in the aggregation procedure. We use the most right hand side map in (4) to define the **global variables**

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} \begin{pmatrix} n_1 \\ n_H \\ n_D \end{pmatrix} = \begin{pmatrix} n_1 \\ n_H + n_D \end{pmatrix} \qquad (6)$$

thus, $n_2(t)$ stands for the total adult population. Moreover, applying the $\mathcal{G}$ map to the auxiliary system yields the **aggregated system**:

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \bar{F}_2 \\ S_1(n_1(t)) & \bar{S}_2 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} \qquad (7)$$




Juvenile survival rate $S_1(n_1)$ depends on juvenile density according to

$$S_1(n_1) = \frac{S_1}{1 + \beta n_1}$$

In addition, escalated contents cause injuries, which entails a decrease in the yearly survival of adults, namely

$$S_i = Se^{-\alpha \bar{C}_i}, \qquad i = H, D$$

where $\bar{C}_i$ is the corresponding average cost of fighting. As doves do not face hawks, doves have no costs. Hawks confront hawks, thus

$$\bar{C}_D = 0 \qquad \bar{C}_H = \frac{C\, n_H}{2\, n_2}$$

where are the average fertility and survival taxes given by

$$\bar{S}_2 = n_H^* S_H + n_D^* S_D \qquad \bar{F}_2 = n_H^* F_H + n_D^* F_D$$

## Main results.

Following [1], the aggregated system (7) provides with useful information about the original system (3) if the time scales are different enough.

**Proposition 2** *System* (7) *has an equilibrium point at*

$$\begin{pmatrix} n_1^* \\ n_2^* \end{pmatrix} = \frac{1}{\beta} \left[ \frac{\bar{F} S_1}{1 - \bar{S}} - 1 \right] \begin{pmatrix} 1 \\ \frac{1}{\bar{F}} \end{pmatrix}$$

*if, and only if, $\bar{F}S + \bar{S} > 1$. In fact, it is is asymptotically stable if, and only if,*

$$\bar{S} + \frac{(1 - \bar{S})^2}{\bar{F} S_1} < 1.$$

**Theorem 1** *There exists a fixed point for the general system* (5) *given by*

$$\boldsymbol{n}^* = \begin{pmatrix} 1 & 0 \\ 0 & n_H^* \\ 0 & n_D^* \end{pmatrix} \begin{pmatrix} n_1^* \\ n_2^* \end{pmatrix}$$

*Moreover, then there exist $r_0 > 0$, $k_0 \in \mathbb{N}$ such that $\forall k \geq k_0$:*

1. *Equation* (3) *has an unique fixed point $\mathbf{n}_k^* \in \bar{B}_{r_0}(\mathbf{n}^*)$*
2. $\lim_{k\to\infty} \mathbf{n}_k^* = \mathbf{n}^*$.

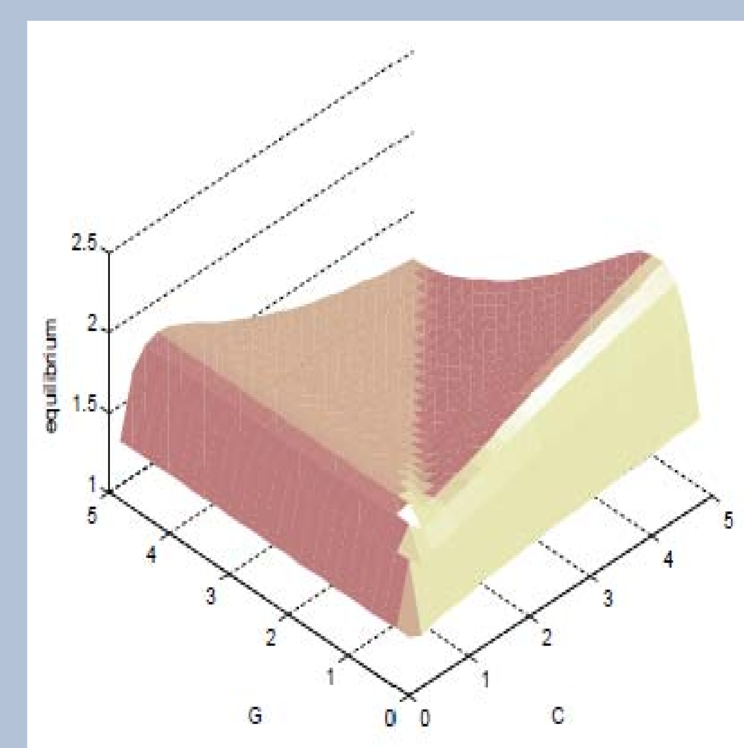
*If, in addition, $(n_1^*, n_2^*) \in \mathbb{R}_+^2$ is hyperbolic*

3. *If $\mathbf{n}^*$ is asymptotically stable (unstable), so is $\mathbf{n}_k^*$.*
4. *Let $\mathbf{n}(0) = (n_1(0), n_H(0), n_D(0)) \in \mathbb{R}_+^3$, if the solution $(n_1(t), n_2(t))$ of* (7) *with initial value $(n_1(0), n_H(0) + n_D(0))$ is such that $\lim_{n\to\infty}(n_1(t), n_2(t)) = (n_1^*, n_2^*)$ then the solution $\mathbf{n}_k(t)$ of* (3) *corresponding to $\mathbf{n}(0)$ verifies $\lim_{t\to\infty} \mathbf{n}_k(t) = \mathbf{n}_k^*$.*

In our model, G represents the quality of the environment, from favorable (low G) to unfavorable (high G). C represents adult ability to provoke weak (low C) or strong (high C) injuries during an escalated contest. The figures show the graph of the function, $n^* = f(G; C)$, with respect to the type of environment G and individual aggressiveness during a contest C, for two different fecundity functions.

For some species the amount of resource has continuous effect on fecundity, for instance, according to a **Holling type fecundity function**

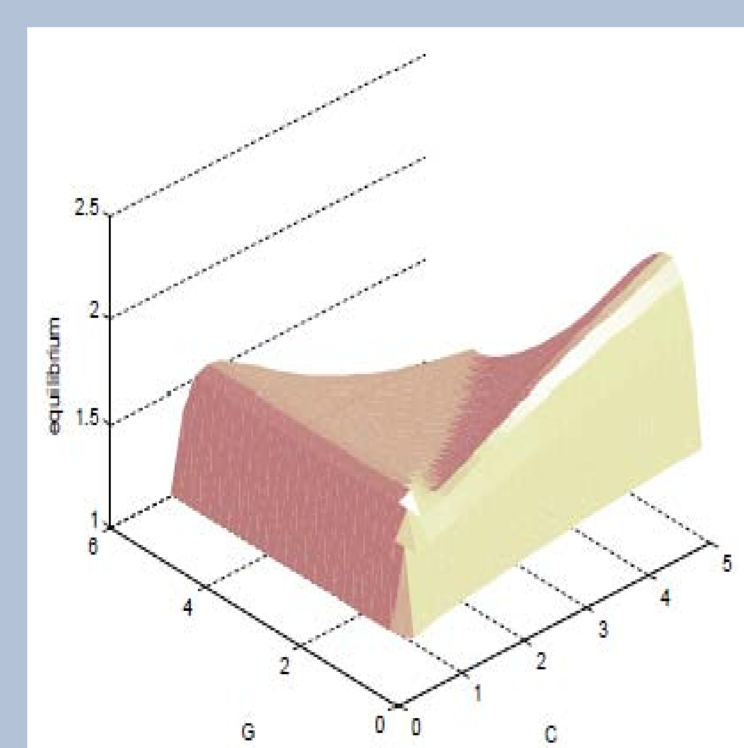
$$F_i(G_i) = \frac{F\bar{G}_i}{\gamma + \bar{G}_i} \qquad i = H, D.$$




$F = 1$; $S = 0.8$; $S_1 = 0.75$; $\alpha = 1.5$; $\beta = 3$; $\gamma = 0.6$

Other species must accumulate certain quantity of resources (**threshold effect**) before reproducing. Thus, according to [2],

$$F_i(G_i) = \frac{F_i}{1 + a/\sqrt{1 + a^2}} \left( \frac{\bar{G}_i - a}{\sqrt{1 + (\bar{G}_i - a)^2}} + \frac{a}{\sqrt{1 + a^2}} \right) \qquad i = H, D.$$




$F = 1$; $S = 0.8$; $S_1 = 0.75$; $\alpha = 1.5$; $\beta = 3$; $\gamma = 0.6$

Where the corresponding $\bar{G}_i$, for $i = H, D$ are given by

$$G < C \quad \Rightarrow \quad \bar{G}_D = \frac{G}{2}\left(1 - \frac{G}{C}\right) \qquad \bar{G}_H = G\left(1 - \frac{G}{2C}\right)$$

$$G > C \quad \Rightarrow \quad \bar{G}_D = 0 \qquad \bar{G}_H = \frac{G}{2}$$

## References

[1] P. Auger, R.Bravo de la Parra, J.C.Poggiale, E.Sánchez and L.Sanz. (2008) *Aggregation methods in dynamical systems and applications in population and community dynamics*, Physics of Life Reviews, **5**, 79–105.

[2] E.Chambon-Dubreuil, J.M.Gilliard, M.Khaladi. (2006). *Effects of aggressive behavior on age-structured population dynamics*. Ecological modelling 193. 777–786.

**The $3^{rd}$ Conference on Computational and Mathematical Population Dynamics. Burdeaux 2010**

Address for correspondence: marcos.marva@uah.es