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A stage structured population model with mature individuals using hawk and dove tactics

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RÉSUMÉ.

ABSTRACT. The purpose of this paper is to investigate the effects of conflicting tactics of resource acquisition on stage structured population dynamics. We present a population subdivided into two distinct stages (immature and mature). We assume that immature individual survival is density-dependent. We also assume that mature individuals acquire resources required to survive and reproduce by using two contrasted behavioral tactics (hawk versus dove). Mature individual survival thus is assumed to depend on the average cost of fights while individual fecundity depends on the average gain in the competition to access the resource. Our model includes two parts: a fast part that describes the encounters and fights involves a game dynamic model based upon the replicator equations, and a slow part that describes the long-term effects of conflicting tactics on the population dynamics. The existence of two time scales allows studying the complete system from a reduced one, which describes the dynamics of the total immature and mature densities at the slow time scale. The analysis of this reduced model shows that proportion of hawks in non-aggressive populations is expected to be larger than in aggressive populations. The maximum fitness (maximum of the total density) in a rich environment is smaller for larger costs.

MOTS-CLÉS : Jeu Faucon-Colombe, Agrégation de variables, dynamique des populations.

KEYWORDS : Hawk and dove game, aggregation of variables, population dynamics.

1. Presentation of the model

We consider a population subdivided into two distinct stages : immature and mature. The immature sub-population do not participate to reproduction. The mature individuals are assume to compete to access resource required for survive and reproduce. Mature reproductive individuals are split into two different tactics : aggressive (hawks) and non-aggressive (doves). Let $n_1(t)$ be the size of the immature population and $n_2(t)$ the total size of the mature individuals population at time t. The model is composed of two parts, a fast part that describes the change of tactics of mature and a slow part that describes the demographic process.

1.1. Fast process : game dynamics.

Mature population is divided into two sub-populations : hawk mature and dove mature. Let $n_2^H(t)$ and $n_2^D(t)$ be respectively the hawk and dove mature individuals densities at time t. The total density of mature is given by $n_2(t) = n_2^H(t)+n_2^D(t)$. Mature individuals are assumed to compete to access resources. This process occurs at the fast time scale.

We use the hawk-dove game in order to represent the interaction between two mature sub-populations. The winner of the game gains an access to a common resource. Therefore, we assume that the gain G is identical for all individuals. C is the cost of loosing an escalated fight. The payoff obtained by hawks and doves when interacting are represented by the classical payoff matrix A (Hofbauer and Sigmund, 1988) :

$$A = \begin{pmatrix} \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix} \qquad [1]$$

Let $x(t)$ and $y(t)$ be respectively the hawks and doves proportions in the mature individuals at time t.

$$x(t) = \frac{n_2^H(t)}{n_2(t)}, \quad y(t) = 1 - x(t) = \frac{n_2^D(t)}{n_2(t)}. \qquad [2]$$

We also use the replicator equations that describe the change of tactics of adult individuals that we now briefly recall. At time t, the gain Δ_H of an individual always using the hawk strategy against a population with a proportion $x(t)$ of hawks and $y(t)$ of doves is the following one :

$$\Delta_H = (1, 0)\, A \begin{pmatrix} x \\ y \end{pmatrix}.$$

The gain Δ_D of an individual always playing the dove strategy is the following one :

$$\Delta_D = (0, 1)\, A \begin{pmatrix} x \\ y \end{pmatrix}.$$

The average gain of an individual playing the two tactics in proportions $(x(t), y(t))$ corresponding to the actual distribution of hawks and doves in the total population is the following one :

$$\Delta = (x, y)\, A \begin{pmatrix} x \\ y \end{pmatrix}.$$

Let us calculate for each tactic, the difference between the gain of each of them and the average gain of the population. If this difference is positive (resp. negative), it is assumed that the proportion of players of this strategy is going to increase, (resp. decrease). With these assumptions, the replicator equations read

$$\left\{\begin{array}{rl} \frac{dx}{d\tau} = & x\left(\Delta_H - \Delta\right) \\ \frac{dy}{d\tau} = & y\left(\Delta_D - \Delta\right) \end{array}\right. \qquad [3]$$

where τ is the fast time scale.

1.2. Slow dynamics : demography.

The assumptions of this model are as follows :

1. The immature population : the birth rate into the immature population is proportional to the existing mature population with a proportionality F ; We further assume that fecundity depends on average gains $\bar{G}_i$, $i = H, D$, the death rate is proportional to the existing immature population with proportionality μ_1. We also assume that the immature individual survival is density-dependent with the negative effect coefficient η.

2. For mature individuals : The transformation rate from the immature individuals to mature individuals is proportional to the existing immature population with proportionality β. For the mature equations, We assume that escalated contests cause injuries and therefore provoke a increase of the mortality of mature individuals according to the following relation : $\mu_2\left(\bar{C}_i\right) = \mu + \alpha\bar{C}_i$, where μ is the constant natural mortality rate supposed identical for hawks and doves, $\bar{C}_i$ is the average cost, $i = H, D$ and α a positive coefficient which permits to regulate the effect of the average cost on the survival. α is a parameter related to environmental conditions.

$$\left\{\begin{array}{rl} \frac{dn_1}{dt} = & F_H(\bar{G}_H)n_2^H + F_D(\bar{G}_D)n_2^D - \mu_1 n_1 - \beta n_1 - \eta n_1^2 \\ \frac{dn_2^H}{dt} = & q\beta n_1 - \mu_2\left(\bar{C}_H\right)n_2^H \\ \frac{dn_2^D}{dt} = & \left(1-q\right)\beta n_1 - \mu_2\left(\bar{C}_D\right)n_2^D \end{array}\right. \qquad [4]$$

Parameter q represents the proportion of immature becoming hawk when surviving to mature (respectively $(1-q)$ for dove). The average cost is calculated by adding the cost of each type of encounter weighted by the proportion of this type of encounter. Therefore, the average cost received by a dove, that we note $\bar{C_D}$ is null, because doves do not fight and do not get injured :

$$\bar{C}_D = 0\frac{n_2^H}{n_2} + 0\frac{n_2^D}{n_2} = 0$$

As a consequence, dove mortality $\mu_2\left(\bar{C_D}\right)$ is simply μ.

$$\mu_2\left(\bar{C}_D\right) = \mu$$

On the contrary, hawks fight and get injured which causes them higher mortality risks than doves. Hawk mortality is a function of the average cost received by a hawk, that we note $\bar{C_H}$:

$$\bar{C}_H = \left(\frac{C}{2}\right)\frac{n_2^H}{n_2} + 0\frac{n_2^D}{n_2} = \left(\frac{C}{2}\right)\frac{n_2^H}{n_2}$$

The hawk mortality $\mu_2\left(\bar{C_H}\right)$ is thus given by the following expression :

$$\mu_2\left(\bar{C}_H\right) = \mu + \alpha\left(\frac{C}{2}\right)\frac{n_2^H}{n_2}$$

1.2.1. Fecundity

We assume that fecundity rates $F(\bar{G}_i)$ depend on the average gains $\bar{G}_i$, for i = H,D, which are calculated as done for the average costs. Doves share gains when meet each other but they get no gain when encounter a hawk, so that

$$\bar{G}_D = 0\frac{n_2^H}{n_2} + \frac{G}{2}\frac{n_2^D}{n_2} = \left(\frac{G}{2}\right)\frac{n_2^D}{n_2} \qquad [5]$$

Hawks share gains when meeting another hawk and they get full gain when encountering a dove, thus

$$\bar{G}_H = \left(\frac{G}{2}\right)\frac{n_2^H}{n_2} + G\frac{n_2^D}{n_2} \qquad [6]$$

First, in order to study the effect of the resource on fecundity, we use a Holling type II function. According to this function, fecundity increases with the average gain and then reaches a plateau. Thus, we choose the following general relationship between fecundity and average gain :

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

We use the average gains of Hawk and Dove of Eqs. (5) and (6) to calculate their respective fecundities. Fecundity is an increasing function of the average gain. Parameter γ permits to influence the “speed” to reach the plateau of the fecundity. When γ decreases the maximum of the fecundity is reached more quickly. γ translates the effect of poor environmental conditions on the fecundity.

1.3. The complete slow–fast model

The complete model is obtained by coupling the previous hawk-dove behavioral model and the populations model as follows :

$$\left\{ \begin{array}{rcl} \frac{dn_1}{d\tau} &=& \varepsilon(F(\frac{\bar{G}_H}{\gamma+\bar{G}_H}n_2^H + \frac{\bar{G}_D}{\gamma+\bar{G}_D}n_2^D) - (\mu_1+\beta)n_1 - \eta n_1^2) \\ \frac{dn_2^H}{d\tau} &=& n_2 x\left(\Delta_H - \Delta\right) + \varepsilon\left(q\beta n_1 - \left(\mu + \alpha\frac{C}{2}\frac{n_2^H}{n_2}\right)n_2^H\right) \\ \frac{dn_2^D}{d\tau} &=& n_2 y\left(\Delta_D - \Delta\right) + \varepsilon\left(\left(1-q\right)\beta n_1 - \mu n_2^D\right) \end{array} \right. \qquad [7]$$

where ε is a small parameter. In this last form, it is obvious that the game dynamics correspond to the fast time scale while the small terms of the order of ε correspond to the slow time scale. This model is a three-dimensional system of ordinary differential equations.

2. The aggregated model

In order to give analytical results of the system occurring on two different time scales, we use aggregation methods (Auger., 1998). These methods related to classical perturbation theory permit the reduction of a system of several state variables at different times scales into a smaller system governing a few global variables, here the total number of immature and mature population. Aggregation methods require here first to solve the fast-time part of system (7) independently and to give its equilibrium points. The aggregated system is then obtained by substitution of the stable equilibrium points into slow-time part of system (7).

2.1. Derivation of the aggregated model

The first step is to neglect the small terms of the order of ε and to look for the existence of a stable equilibrium for the fast part of the system which relates to the game dynamics

$$\left\{ \begin{array}{ll} \frac{dx}{d\tau} = & x\left(\Delta_H - \Delta\right) \\ \frac{dy}{d\tau} = & y\left(\Delta_D - \Delta\right) \end{array} \right.$$

Using the fact that $x+y=1$ at any time t and after some algebra, the previous system can be reduced to a single equation governing the hawk proportion of individual. In case of constant gains and costs, it reads

$$\frac{dx}{d\tau} = \frac{x}{2}\left(1-x\right)\left(G - Cx\right). \qquad [8]$$

This equation has three equilibria, $0, 1$ and $\frac{G}{C}$. 0 is always unstable. Let us denote x^* the stable non-trivial equilibrium. According to parameters values, two cases can occur :

► $G < C$, $x^* = \frac{G}{C}$ is asymptotically stable for any initial condition $0 < x(0) < 1$. In this case, at equilibrium, the population is polymorphic with a proportion $\frac{G}{C}$ of hawks and $1 - \frac{G}{C}$ of doves.

When replacing the variables n_2^H and n_2^D by those of the fast equilibrium, the average costs and gains become :

$$\begin{array}{ll} \bar{C}_H = \frac{G}{2} & \bar{C}_D = 0 \\ \bar{G}_H = G\left(1 - \frac{G}{2C}\right) & \bar{G}_D = \frac{G}{2}\left(1 - \frac{G}{C}\right) \end{array}$$

► $G > C$, $x^* = \frac{G}{C}$ does not belong to the interval $[0, 1]$. The equilibrium 1 is asymptotically stable. The population is monomorphic and totally hawk at equilibrium.
When replacing the variables n_2^H and n_2^D of the complete model by those of the fast equilibrium, the average costs and gains become :

$$\begin{array}{ll} \bar{C}_H = \frac{C}{2} & \bar{C}_D = 0 \\ \bar{G}_H = \frac{G}{2} & \bar{G}_D = 0 \end{array}$$

In order to aggregate, we make the assumption that the fast process is at the fast equilibrium. Thus, we come back to the complete initial system (7), substitute the previous fast equilibrium and add the two matures equations. It is necessary to replace the fast variables in terms of the fast equilibrium as follows :

$$n_2^H = x^* n_2 \quad \text{and} \quad n_2^D = (1 - x^*) n_2$$

After some algebra, one obtains the following system of two equations governing the immature and mature densities at the slow time scale, that we call the aggregated model

$$\left\{ \begin{array}{ll} \frac{dn_1}{dt} = & F\left(\frac{\bar{G}_H}{\gamma + \bar{G}_H} x^* + \frac{\bar{G}_D}{\gamma + \bar{G}_D}(1 - x^*)\right) n_2 - (\mu_1 + \beta)\, n_1 - \eta n_1^2 \\ \frac{dn_2}{dt} = & \beta n_1 - \mu n_2 - \alpha \frac{C}{2}\left(x^*\right)^2 n_2 \end{array} \right. \qquad [9]$$

The dynamics of system (9) are a good approximation of the real dynamics if two conditions are met :
• The system is structurally stable, which is the case.
• ε is small enough, which is assumed.

In our case, we remember that we can have two possibilities for the fast equilibrium, then we obtain two different aggregated models which are valid on two domains of the phase plane :

• Model I : $G < C$, $x^* = \frac{G}{C}$ is asymptotically stable in Eq. (8),

$$\left\{ \begin{array}{rcl} \frac{dn_1}{dt} &=& F\left(\frac{\bar{G}_H}{\gamma+\bar{G}_H}\frac{G}{C} + \frac{\bar{G}_D}{\gamma+\bar{G}_D}(1-\frac{G}{C})\right)n_2 - (\mu_1+\beta)\,n_1 - \eta n_1^2 \\ \frac{dn_2}{dt} &=& \beta n_1 - \mu n_2 - \alpha\frac{G^2}{2C}n_2 \end{array} \right. \qquad [10]$$

where

$$\bar{G}_H = G\left(1-\frac{G}{2C}\right), \quad \bar{G_D} = \frac{G}{2}\left(1-\frac{G}{C}\right)$$

• Model II : $G > C$, $x^* = 1$ is asymptotically stable in Eq. (8),

$$\left\{ \begin{array}{rcl} \frac{dn_1}{dt} &=& F\frac{\bar{G}_H}{\gamma+\bar{G}_H}n_2 - (\mu_1+\beta)\,n_1 \\ \frac{dn_2}{dt} &=& \beta n_1 - \mu n_2 - \alpha\frac{C}{2}n_2 \end{array} \right. \qquad [11]$$

where $\bar{G}_H = \frac{G}{2}$.

It must be noted that there is continuity, i.e. average gains and costs in mixed and pure hawk cases become equal at the separation line between the two models, when $G = C$, in this case These two models connect.

2.2. Study of the dynamics of the aggregated model

We set up the stage structured model with general form

$$\left\{ \begin{array}{rcl} \frac{dn_1}{dt} &=& F_1 n_2 - (\mu_1+\beta)\,n_1 - \eta n_1^2 = P(n_1,n_2) \\ \frac{dn_2}{dt} &=& \beta n_1 - r n_2 = Q(n_1,n_2) \end{array} \right. \qquad [12]$$

where $F_1 = F\left(\frac{\bar{G}_H}{\gamma+\bar{G}_H}\frac{G}{C} + \frac{\bar{G}_D}{\gamma+\bar{G}_D}(1-\frac{G}{C})\right)$, $r = \mu + \alpha\frac{G^2}{2C}$ in the case of mixed strategy and $F_1 = F\frac{\bar{G}_H}{\gamma+\bar{G}_H}$, $r = \mu + \alpha\frac{C}{2}$ in the case of pure hawk population.

Considering the biological significance, we study system (12) in the region

$$D = \left\{(n_1,n_2) \in R^2 : n_1 \geq 0, n_2 \geq 0\right\}.$$

The initial conditions for system (12) take the form of

$$n_1(0) > 0, n_2(0) > 0. \qquad [13]$$

2.2.1. Analysis of equilibria

A simple study shows that the aggregated model has 2 equilibria :

1. The origin (0, 0) is stable if $F_1\beta < r(\mu_1+\beta)$
2. The interior equilibrium point $P_1(n_1^*, n_2^*)$ which is given by

$$n_1^* = \frac{F_1\beta - r\,(\mu_1+\beta)}{r\eta}, \quad n_2^* = \frac{\beta}{r}n_1^*.$$

and which is globally asymptotically stable if $F_1\beta > r(\mu_1+\beta)$

Details of local stability analysis are not shown because the aggregated model is a classical model.

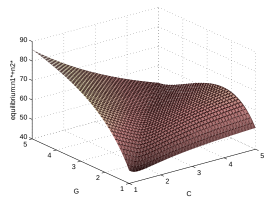

Figure 1. *Equilibrium n^* as a function of gain (G) and cost (C) considering Holling type fecundity function. Parameter values $F = 1$, $\beta = 0.25, \gamma = 0.6, \mu = 0.03, \alpha = 0.005$.*

3. Discussion

Our results are represented in a synthetic manner on figures 1 and 2 displaying the total population density at the equilibrium when a Holling fecundity function is considered. The total population density can be understood as a measure of the population fitness with respect to game parameters that relate to individual behavior, the gain G and the cost C. Namely, we consider here that populations having the largest total density at equilibrium might have a better chance to survive in the long term. Therefore, we assume that individuals would try to find an environment that maximizes the total population density in the long term. In our model G, the gain of the game, can be seen as the resource biomass that is obtained when an individual is the winner of a contest. Therefore, a gradient of gain G can be considered as a gradient of resource abundance from poor (associated with small gains) to rich (associated with large gains) environments. A gradient of cost can be considered as a measure of individual aggressiveness, from few aggressive individuals or species (associated with small costs) to very aggressive specimens (associated with large costs). Each plotting displayed in figures 1 and 2 is composed of two parts that should

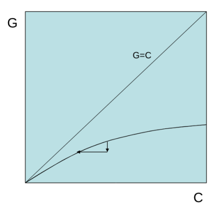

Figure 2. *Hill curve of local maxima and the effect of global change and human activities on the population size. As G decreases, the population size leaves the top of the hill. Reducing aggressiveness, C, will let the population reach the maximum fitness at the top of the hill.*

be considered separately below and above the bisectrix $G = C$. Indeed, when $G > C$, the mature population is pure hawk while in the domain $G < C$, the population is mixed with a constant proportion of hawks at the fast equilibrium $G = C$. In the first domain, $G > C$, the total population fitness is a monotone increasing function of G at fixed cost. This signifies that the population fitness always increases when the environment is richer and this makes sense. On the contrary, at fixed gain G, the population fitness increases for smaller costs. Therefore, in a pure hawk population, as expected, the total fitness increases when the matures are less aggressive leading to less injuries and to smaller mortality. In the second domain, $G < C$, the population is mixed with hawks and doves. In that domain, if one keeps constant the cost C, we observe a maximum of the population fitness when the gain increases from zero. Therefore, the model predicts that according to the level of aggressiveness of the population, there is a particular type of environment that maximizes the population fitness. Similarly, if one keeps the gain G constant, there is a cost that maximizes the population fitness. In other words, in a given environment, there is a level of aggressiveness in the population that maximizes the population fitness. Moreover, figures 1 and 2 show a curve of local maxima associated with a hill line observed in the domain $G < C$. It is important to note that the population fitness along this hill increases for larger gains and costs. Therefore, it signifies that populations might increase their fitness by choosing to settle in a better environment (larger G) as well as by adopting a more aggressive behavior (larger C). However, the hill curve has a slope that slightly decreases when C increases. Therefore, the population fitness is increased for populations in which the proportion of aggressive individuals decreases when the cost becomes larger. In other words, the model predicts that when the cost is high, the proportion of aggressive individuals should be smaller in order to maximize the population fitness.

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