INFLUENCE OF INDIVIDUAL AGGRESSIVENESS ON THE DYNAMICS OF COMPETITIVE POPULATIONS

Eva Sanchez[1], Pierre Auger[2], Rafael Bravo de la Parra[3]

[1] Dpto Matemáticas, ETSI Industriales, UPM, Madrid, Spain
[2] UMR CNRS 5558, University Claude Bernard, Lyon-1, France
[3] Departamento de Matematicas, Universidad de Alcala de Henares, Spain

ABSTRACT

Two populations are subdivided into two categories of individuals (hawks and doves). Individuals fight to have access to a resource which is necessary for their survival. Conflicts occur between individuals belonging to the same population and to different populations. We investigate the long term effects of the conflicts on the stability of the community. The model is a set of ODE's with four variables corresponding to hawk and dove individuals of the two populations. Two time scales are considered. A fast time scale is used to describe frequent encounters and fightings between individuals trying to monopolize the resource. A slow time scale is used for the demography and the long term effects of encounters. We use aggregation methods in order to reduce this model into a system of two ODE's only for the total densities of the two populations which is found to be a classical Lotka-Volterra competition model. We study different cases of proportions of hawks and doves in both populations on the global coexistence and the mutual exclusion of the two populations. Pure dove tactics in both populations are unstable. In cases of mixed hawk and dove in both populations, there is coexistence. Pure dove or mixed hawk-dove tactics in one population can coexist with pure hawks in the other one when the costs of fightings between hawks are large enough.

1. INTRODUCTION

An important aspect of population dynamics is the study of the effects of different individual tactics on the stability of the community. In this work, we consider two populations competing for a resource which is necessary for their survival. Individuals encounter frequently (for example several times per day) and use classical hawk and dove tactics to have an access to the resource (Hofbauer & Sigmund, 1988; Maynard-Smith, 1982). The hawk is aggressive in all cases. The dove avoids to fight against a hawk. As a consequence, a hawk is the winner against a dove. But when hawks meet, they fight and this may induce severe injuries and possibly their death. When doves meet, they don't fight and one of them gets access to the resource. In the classical hawk-dove game, when the cost is larger than the gain, a mixed situation occurs with constant proportions of hawks and doves at equilibrium.

In this contribution two populations are considered, each one being composed of hawks

Acta Biotheoretica **45**: 321–333, 1997.

and doves. Fightings occur between individuals of the same population but also between individuals of the two populations. The payoff matrix is a 4×4 matrix. The winner has access to the resource which corresponds to the gain G. This gain is assumed to be the same for individuals of both populations. Intra-population costs C due to hawk-hawk conflicts are also assumed to be the same for both populations. But, inter-population costs C_{12} and C_{21} are different. For example, if $C_{12} > C_{21}$, hawks of population 1 can provoke more important injuries to hawks of population 2 than the reverse.

Furthermore, two time scales are considered. As individuals must feed every day and need to have access to the resource frequently, we assume that the game dynamics occur at a fast time scale. A slow time scale is used for describing the demography and the long term effects of encounters. Thus, the model is in two parts, a fast part describing intra and inter-population game dynamics and a slow part describing the demography and the long term effects of encounters on the growth of the populations.

This model is composed of four ODE's governing the hawk and dove subpopulations of the two populations. Aggregation methods are used in order to reduce the dimension of a system of ODE's (see Iwasa *et al.*, 1987, 1989). In this article, we use aggregation methods based on perturbation technics which allow us to get a system of ODE's for the total densities of populations at a slow time scale (see Auger & Roussarie, 1994). This method takes into account the hierarchical structure of the system (Auger, 1989) and has been used in the context of population dynamics for time discrete models (Bravo de la Parra *et al.*, 1995; Sanchez *et al.*, 1995) as well as for time continuous models (Auger & Poggiale, 1995, 1996). In this work, the aggregated model is found to be a classical Lotka-Volterra competition model. The aim of this article is to study the effects of different proportions of hawk and dove individuals, at the fast equilibrium, on coexistence or exclusion of the populations in the long term. To start with, let us present the general model.

2. THE GENERAL MODEL

We consider a community of two populations each of them being structured into two subpopulations corresponding, respectively, to individuals using hawk (H) and dove (D) tactics. It is assumed that individuals compete for a resource. Competitive interactions exist between individuals of the same population (intraspecific competition) and between individuals of the two populations (interspecific competition). At each particular encounter, the gain of the game corresponds to the access to the resource. Individuals frequently change tactics from one encounter to the next. Thus, according to different encounters, the same individual can use hawk or dove tactics. The general model is composed of two parts, the fast part which describes the change of strategy and the slow part which describes the long-term effects of the conflicts on the growth of the sub-populations.

2.1 Fast part: game dynamics

As the winner of a game has an access to a unique resource, we assume that the gain G is identical for all individuals of both populations. The fast part of the model describes the game dynamics and corresponds to a classical H-D game matrix A :

$$A = \begin{bmatrix} \frac{G-C}{2} & G & \frac{G-C_{12}}{2} & G \\ 0 & \frac{G}{2} & 0 & \frac{G}{2} \\ \frac{G-C_{21}}{2} & G & \frac{G-C}{2} & G \\ 0 & \frac{G}{2} & 0 & \frac{G}{2} \end{bmatrix} \tag{1}$$

We also assume that the costs C due to injuries of hawks conflicts are identical within both populations. Asymmetry comes from different costs incurred when a hawk encounters another hawk of the other population. Let C_{12} (resp. C_{21}) be the cost when a hawk of population 1 (resp. 2) fights against a hawk of population 2 (resp. 1). Let n_α^H and n_α^D be respectively the hawk and dove sub-populations of population α, $\alpha = 1,2$. n_α is the total population α, *i.e.* $n_\alpha = n_\alpha^H + n_\alpha^D$. Let x_1^H and x_1^D (resp. x_2^H and x_2^D) be the proportions of hawks and doves in the total population 1 (resp. 2):

$$x_1^H = \frac{n_1^H}{n_1}, \quad x_2^H = \frac{n_2^H}{n_2}, \quad x_1^D = \frac{n_1^D}{n_1}, \quad x_2^D = \frac{n_2^D}{n_2}. \tag{2}$$

The next set of differential equations describes the change of the H and D proportions:

$$\frac{dx_1^H}{dt} = x_1^H \left((1,0,0,0)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T - \left(x_1^H,x_1^D,0,0\right)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T\right), \tag{3a}$$

$$\frac{dx_1^D}{dt} = x_1^D \left((0,1,0,0)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T - \left(x_1^H,x_1^D,0,0\right)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T\right), \tag{3b}$$

$$\frac{dx_2^H}{dt} = x_2^H \left((0,0,1,0)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T - \left(0,0,x_2^H,x_2^D\right)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T\right), \tag{3c}$$

$$\frac{dx_2^D}{dt} = x_2^D \left((0,0,0,1)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T - \left(0,0,x_2^H,x_2^D\right)A\left(x_1^H,x_1^D,x_2^H,x_2^D\right)^T\right). \tag{3d}$$

Each individual changes tactics at a fast time-scale and thus compares the different tactics in its life. System (3) describes the dynamics of the proportions of individuals using the different strategies. These equations are the classical replicator equations (Hofbauer & Sigmund, 1991). The proportions of individuals of population 1 playing H, *i.e.* x_1^H, increases when the payoff of an individual always using strategy H is higher than the average payoff of an individual playing H in the proportion x_1^H and D in the proportion x_1^D.

One must note that $x_1^H + x_1^D = 1$ and $x_2^H + x_2^D = 1$. Consequently, system (3) reduces to two equations (4):

$$\begin{aligned} \frac{dx}{dt} &= \frac{x}{2}(1-x)(2G-Cx-C_{12}y), \\ \frac{dy}{dt} &= \frac{y}{2}(1-y)(2G-Cy-C_{21}x), \end{aligned} \tag{4}$$

in which $x = x_1^H$ and $y = x_2^H$.

2.2 Slow part: growth of the sub-populations

For each sub-population (H and D) of any population, the slow part is composed of two terms, a linear growth term and negative quadratic terms taking into account long term negative effects of encounters. The growth of each sub-population is thus described as follows:

$$\frac{dn_1^H}{dt} = \frac{r}{2}n_1 - k_{11}^H n_1^H n_1^H - k_{11}^{HD} n_1^H n_1^D - k_{12}^H n_1^H n_2^H - k_{12}^{HD} n_1^H n_2^D, \tag{5-a}$$

$$\frac{dn_1^D}{dt} = \frac{r}{2}n_1 - k_{11}^{DH} n_1^D n_1^H - k_{11}^D n_1^D n_1^D - k_{12}^{DH} n_1^D n_2^H - k_{12}^D n_1^D n_2^D, \tag{5-b}$$

$$\frac{dn_2^H}{dt} = \frac{r}{2}n_2 - k_{21}^H n_2^H n_1^H - k_{21}^{HD} n_2^H n_1^D - k_{22}^H n_2^H n_2^H - k_{22}^{HD} n_2^H n_2^D, \tag{5-c}$$

$$\frac{dn_2^D}{dt} = \frac{r}{2}n_2 - k_{21}^{DH} n_2^D n_1^H - k_{21}^D n_2^D n_1^D - k_{22}^{DH} n_2^D n_2^H - k_{22}^D n_2^D n_2^D. \tag{5-d}$$

r is the growth rate of both populations. The quadratic terms take into account the negative effects of encounters between individuals in the same population and between different populations.

It is also assumed that the k-parameters are proportional to the difference between the gain G and the coefficient of the game matrix associated to this particular event. For example, k_{12}^{HD} corresponds to the encounter of a hawk of population 1 with a dove of population 2 and consequently, $k_{12}^{HD} = \delta(G - a_{14})$ where a_{14} is an entry of the payoff matrix A and δ is the proportionality constant. By this assumption, when the player wins G, the k value is equal to zero, it has unrestricted access to the resource and this particular encounter has no negative effects on its growth. Substitution of the payoff matric coefficients into the previous expressions leads to:

$$k_{11}^H = k_{22}^H = \delta\left(\frac{G+C}{2}\right), \quad k_{12}^H = \delta\left(\frac{G+C_{12}}{2}\right), \quad k_{21}^H = \delta\left(\frac{G+C_{21}}{2}\right) \tag{6-a}$$

$$k_{11}^{DH} = k_{22}^{DH} = k_{12}^{DH} = k_{21}^{DH} = \delta(G), \tag{6-b}$$

$$k_{11}^{D} = k_{22}^{D} = k_{12}^{D} = k_{21}^{D} = \delta\left(\frac{G}{2}\right), \tag{6-c}$$

$$k_{11}^{HD} = k_{22}^{HD} = k_{12}^{HD} = k_{21}^{HD} = 0. \tag{6-d}$$

2.3 The complete model

The complete model is obtained by adding the fast part (eq.(4)) and the slow part (eq.5)). Two essential features to be taken into account are:

1) The fact that the game dynamics is fast is modelled by multiplying the rates by a large number.

2) Each of the subpopulations 1 and 2 is constant through time, that is to say, n_1 = constant and n_2 = constant. With these remarks in mind, straightforward computations lead to the following system of equations:

$$\varepsilon\frac{dn_1^H}{dt} = n_1\left(\frac{x}{2}(1-x)(2G-Cx-C_{12}y)\right) + \varepsilon\frac{r}{2}n_1 - \varepsilon n_1^H\left(k_{11}^H n_1^H + k_{11}^{HD} n_1^D + k_{12}^H n_2^H + k_{12}^{HD} n_2^D\right), \tag{7-a}$$

$$\varepsilon\frac{dn_1^D}{dt} = -n_1\left(\frac{x}{2}(1-x)(2G-Cx-C_{12}y)\right) + \varepsilon\frac{r}{2}n_1 - \varepsilon n_1^D\left(k_{11}^{DH} n_1^H + k_{11}^{D} n_1^D + k_{12}^{DH} n_2^H + k_{12}^{D} n_2^D\right), \tag{7-b}$$

$$\varepsilon\frac{dn_2^H}{dt} = n_2\left(\frac{y}{2}(1-y)(2G-Cy-C_{21}x)\right) + \varepsilon\frac{r}{2}n_2 - \varepsilon n_2^H\left(k_{21}^H n_1^H + k_{21}^{HD} n_1^D + k_{22}^H n_2^H + k_{22}^{HD} n_2^D\right), \tag{7-c}$$

$$\varepsilon\frac{dn_2^D}{dt} = -n_2\left(\frac{y}{2}(1-y)(2G-Cy-C_{21}x)\right) + \varepsilon\frac{r}{2}n_2 - \varepsilon n_2^D\left(k_{21}^{DH} n_1^H + k_{21}^{D} n_1^D + k_{22}^{DH} n_2^H + k_{22}^{D} n_2^D\right), \tag{7-d}$$

3. DERIVATION OF THE AGGREGATED MODELS

3.1 Asymptotic properties of the fast dynamics

The fast system is governed by the two ordinary differential equations (4). Our variables x and y vary in the interval $[0,1]$. Thus, the domain of study is a square $[0,1]\times[0,1]$. The steady states are the points $(0,0)$, $(0,1)$, $(1,0)$, $(1,1)$, $(\frac{2G}{C},0)$, $(0,\frac{2G}{C})$, $(1,\frac{2G-C_{21}}{C})$, $(\frac{2G-C_{12}}{C},1)$, $\left(\frac{2G(C-C_{12})}{C^2-C_{12}C_{21}}, \frac{2G(C-C_{21})}{C^2-C_{12}C_{21}}\right) = (x^*,y^*)$ inside the domain (according to parameters values).

3.2 Aggregated competition models

Let $(\bar{x},\bar{y})$ be the equilibrium point of the fast dynamics (4). The general form of the aggregated model is as follows, see appendix I:

$$\begin{aligned} \frac{dn_1}{dt} &= rn_1(1-\alpha_1 n_1-\alpha_{12}n_2), \\ \frac{dn_2}{dt} &= rn_2(1-\alpha_2 n_2-\alpha_{21}n_1), \end{aligned} \tag{8}$$

and we have the following expressions:

$$\begin{aligned} \alpha_1 &= \frac{\delta}{2r}\left(C(\bar{x})^2 + G\right), \quad \alpha_2 = \frac{\delta}{2r}\left(C(\bar{y})^2 + G\right), \\ \alpha_{12} &= \frac{\delta}{2r}\left(C_{12}(\overline{xy}) - G\bar{x}+G\bar{y}+G\right), \\ \alpha_{21} &= \frac{\delta}{2r}\left(C_{21}(\overline{xy})+G\bar{x}-G\bar{y}+G\right), \end{aligned} \tag{9}$$

Now, we proceed to the following change of variables:

$$\begin{aligned} u_1 &= \frac{\delta}{2r}\left(C(\bar{x})^2+G\right)n_1, \\ u_2 &= \frac{\delta}{2r}\left(C(\bar{y})^2+G\right)n_2, \end{aligned} \tag{10}$$

which allows to rewrite system (8) in the normalized form (11):

$$\begin{aligned} \frac{du_1}{dt} &= ru_1(1-u_1-a_{12}u_{12}), \\ \frac{du_2}{dt} &= ru_2(1-u_2-a_{21}u_1), \end{aligned} \tag{11}$$

in which the competition coefficients are as follows:

$$\begin{aligned} a_{12} &= \frac{C_{12}(\overline{xy})-G\bar{x}+G\bar{y}+G}{C(\bar{y})^2+G}, \\ a_{21} &= \frac{C_{21}(\overline{xy})+G\bar{x}-G\bar{y}+G}{C(\bar{x})^2+G}. \end{aligned} \tag{12}$$

The aggregated model is a classical Lotka-Volterra model. Consequently, (0,0), (1,0), (0,1) and (u_1^*, u_2^*) are equilibrium points. The last point is defined by the following equations:

$$u_1^* = \frac{1-a_{12}}{1-a_{12}a_{21}}, \qquad u_2^* = \frac{1-a_{21}}{1-a_{12}a_{21}}, \tag{13}$$

4. COEXISTENCE OR EXCLUSION IN RELATIONSHIP TO AGGRESSIVENESS

First of all, the equilibrium point (0,0) of system (4) is never stable. This means that two populations using pure dove tactics cannot occur. Part of the individuals of at last one of the two populations must use the hawk strategy.

4.1 The case where no population is pure hawk

$x = 0$, $x = 1$, $y = 0$ and $y = 1$ are nullclines. Consequently, the square $[0,1]\times[0,1]$ is positively invariant and the ω-limit set is an equilibrium point of this domain because the system is competitive, for proof see page 158, (Hofbauer & Sigmund, 1991). One can distinguish the following four cases:

a) When (x^*,y^*) is globally asymptotically stable, g.a.s. (i.e. for any initial condition in $]0,1[\times]0,1[$, the trajectory tends to (x^*,y^*)), then the two populations always coexist (see appendix II).

b) When $(\frac{2G}{C},0)$ and $(0,\frac{2G}{C})$ belong to the square $]0,1[\times]0,1[$, three cases can occur:

- $C_{12} < C < C_{21}$ and $2G<C$: $(\frac{2G}{C},0)$ is g.a.s.
- $C_{21} < C < C_{12}$ and $2G<C$: $(0,\frac{2G}{C})$ is g.a.s.
- $C_{12} > C$ and $C_{21} > C$ and $2G<C$: $(\frac{2G}{C},0)$ and $(0,\frac{2G}{C})$ are both asymptotically stable. A separatrix divides the domain into two parts corresponding to two basins of attraction. A calculation, given in appendix II, shows that for the three different cases, we have the following result:

$$0 < a_{12} < 1, \quad 0 < a_{21} < 1, \tag{14}$$

This means that the point (u_1^*,u_2^*) is globally asymptotically stable. The two populations coexist in any case. In summary of this subsection, when none of the two populations is pure hawk, they always coexist.

4.2 The case where one population is pure hawk

When (0,1) is g.a.s., the equation of population 2 in the aggregated system reduces to a logistic equation because $a_{21} = 0$. Thus, its density tends to its carrying capacity. For population 1, two cases can occur, see appendix II:

- Either $C>G$; then, there exists a point (u_1^*,u_2^*) which is globally asymptotically stable. Both populations coexist, Fig. 1.
- Or, $C<G$; population 1 gets extinct and population 2 goes to its carrying capacity, Fig. 2.

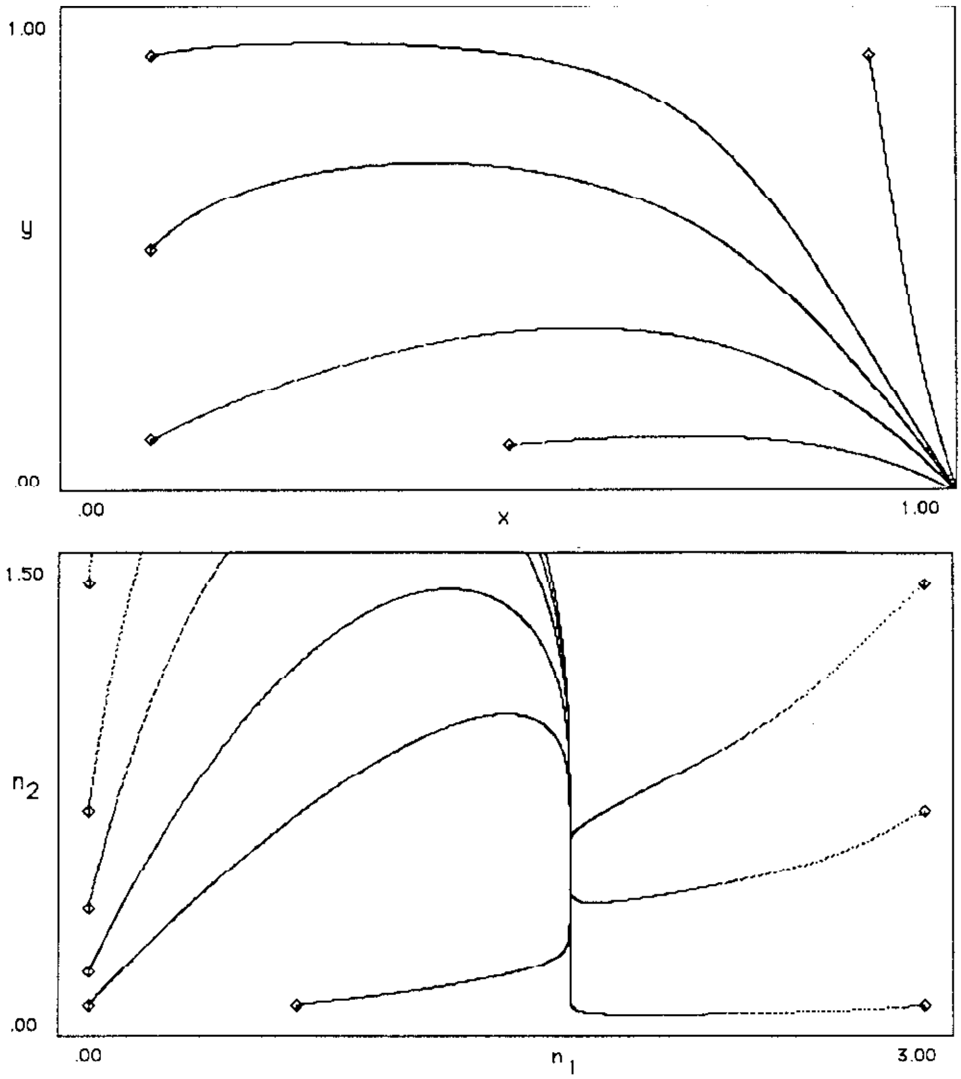

Fig.1.: $G = 3/2$, $C = 2$, $C_{12} = 1$, $C_{21} = 4$. a) The fast system tends to the fixed point (1,0) which corresponds to individuals using the hawk strategy in population 1 and the dove one in population 2. b) Runge-Kutta simulation of the full system (7). At each time, hawk and dove subpopulations are added to obtain the total densities. This figure shows that the two populations coexist.

The point (1,0) exhibits similar results.

- When one of the equilibrium points $(1, \frac{2G-C_{21}}{C})$ or $(\frac{2G-C_{12}}{C},)$ is stable, according to parameters values, the populations can either coexist or mutually exclude. We do not make explicit these domains of the parameters.

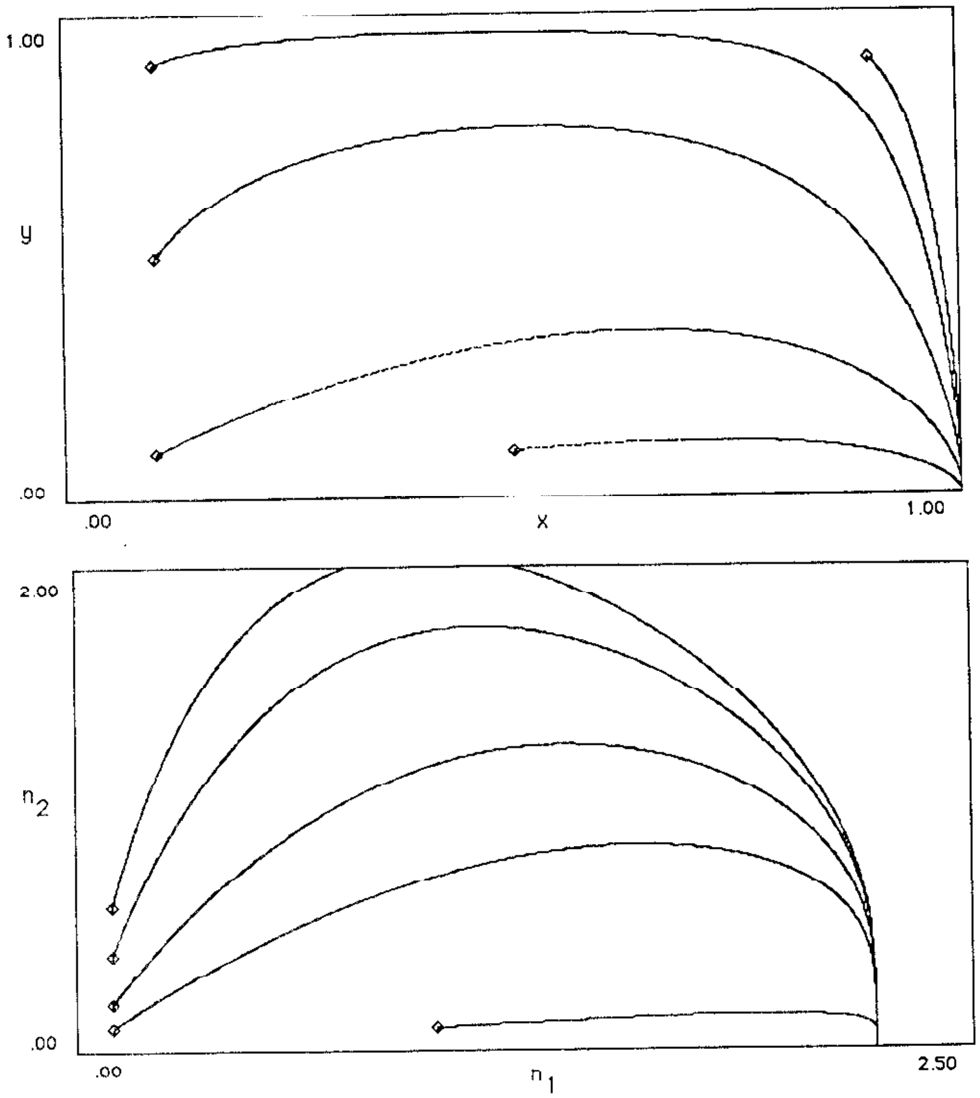

Fig.2. $G = 3/2$, $C = 1.2$, $C_{12} = 1$, $C_{21} = 4$. a) Similarly to the case of figure 1, the fast system tends to the fixed point (1,0). Population 1 is hawk and population 2 dove. b) Runge-Kutta simulation of the full system (7). Contrary to the case of figure 1, the dove population gets extinct.

In summary of this subsection, when one of the two populations is pure hawk, we may have either coexistence or extinction of the population with hawks and doves.

4.3 The case of all aggressive individuals

When the point (1,1) is g.a.s. for system (4), i.e. when all the individuals of both populations at the fast equilibrium are hawks, one can calculate the competition coefficients from equations (12) of the aggregated Lotka-Volterra model as follows:

$$a_{12} = \frac{C_{12}+G}{C+G}, \quad a_{21} = \frac{C_{21}+G}{C+G} \tag{15}$$

Consequently, in the case of all individuals being aggressive, four cases occur:

a) $C_{12} < C$ and $C_{21} < C$; then, $0 < a_{12} < 1$, and $0 < a_{21} < 1$; there is coexistence.

b) $C_{12} > C$ and $C_{21} > C$; then $a_{12} > 1$, and $a_{21} > 1$; there is exclusion. There is a separatrix. According to initial conditions, either 1 or 2 wins.

c) $C_{12} < C$ and $C_{21} > C$; then $0 < a_{12} < 1$, and $a_{21} > 1$; there is exclusion, 1 wins.

d) $C_{12} > C$ and $C_{21} < C$; then $a_{12} > 1$, and $0 < a_{21} < 1$; there is exclusion, 2 wins.

The conclusion of this subsection is that when all individuals are aggressive, they can coexist only when the costs of the interpopulation conflicts between hawks are lower than the costs within the same population. In order to coexist, interpopulation injuries must be weaker than intra-population ones. This effect minimizes the costs globally and leads to coexistence.

5. CONCLUSION

This work shown the following results:

- Two pure dove populations cannot occur.
- Two populations with both doves and hawks always coexist.
- Mutual exclusion only occurs when at least one of the two populations is pure hawk.
- In the case of mutual exclusion, the surviving population is always a pure hawk one.

In view of these conclusions, the hawk strategy has an advantage with respect to the dove one because a pure hawk population cannot get extinct when it encounters a mixed hawk population. However, the study of the case of all aggressive individuals shows that when two pure hawk populations encounter, one of them can get extinct. Thus, one can understand that all populations are not pure hawks and that pure dove and mixed populations can also maintain.

In this article, we have limited our study to particular situations, i.e. when all the gains are equal and when the intra-population costs are equal for the two populations. In the near future, we intend to continue this study and to obtain the solutions in more general cases. The method that we have presented in this article can also be extended to more than two tactics, to more than two populations and to density-dependent game dynamics.

APPENDIX I: DERIVATION OF THE AGGREGATED MODEL

We start with model (7).

The fast part is conservative, i.e. $n_\alpha = n_\alpha^H + n_\alpha^D$, $\alpha = 1,2$ are constant of motion for the game dynamics. Adding equations (7-a) and (7-b) together on the one hand; and (7-c) and (7-d) on the other hand, leads to two equations for the total densities n_1 and n_2:

$$\frac{dn_1}{dt} = rn_1 + n_1^H\left(k_{11}^H n_1^H - k_{11}^{HD} n_1^D - k_{12}^H n_2^H - k_{12}^{HD} n_2^D\right)$$
$$+ n_1^D\left(k_{11}^{DH} n_1^H - k_{11}^D n_1^D - k_{12}^{DH} n_2^H - k_{12}^D n_2^D\right),$$
$$\frac{dn_2}{dt} = rn_2 + n_2^H\left(k_{21}^H n_1^H - k_{21}^{HD} n_1^D - k_{22}^H n_2^H - k_{22}^{HD} n_2^D\right)$$
$$+ n_2^D\left(k_{21}^{DH} n_1^H - k_{21}^D n_1^D - k_{22}^{DH} n_2^H - k_{22}^D n_2^D\right),$$

Then, we assume the existence of a g.a.s. fast equilibrium $(\bar{x},\bar{y})$. To get the aggregated model, we must replace the hawk and dove subpopulations in terms of this fast equilibrium as follows:

$$n_1^H = \bar{x}n_1, \quad n_1^D = (1-\bar{x})n_1, \quad n_2^H = \bar{y}n_2, \quad n_2^D = (1-\bar{y})n_2,$$

Then substitution of these expressions into the previous equations $\left(\frac{dn_1}{dt}, \frac{dn_2}{dt}\right)$ with relations (6) leads to the aggregated slow model (8) governing the total densities of the populations:

$$\frac{dn_1}{dt} = rn_1(1 - \alpha_1 n_1 - \alpha_{12} n_2),$$
$$\frac{dn_2}{dt} = rn_2(1 - \alpha_2 n_2 - \alpha_{21} n_1), \qquad (8)$$

where we have the following expressions (9) of the main text:

$$\alpha_1 = \frac{\delta}{2r}\left(C(\bar{x})^2 + G\right), \quad \alpha_2 = \frac{\delta}{2r}\left(C(\bar{y})^2 + G\right),$$
$$\alpha_{12} = \frac{\delta}{2r}(C_{12}(\overline{xy}) - G\bar{x} + G\bar{y} + G), \qquad (9)$$
$$\alpha_{21} = \frac{\delta}{2r}(C_{21}(\overline{xy}) + G\bar{x} - G\bar{y} + G).$$

APPENDIX II: CALCULATION OF THE COMPETITION COEFFICIENTS OF THE AGGREGATED MODEL

The competition coefficients are given in equations (12).

As both $\bar{x},\bar{y}$ are less than 1 (they are proportions), it is obvious that a_{12} and $a_{21} > 0$.

II.1 Equilibrium point $(x^*,y^*) = \left(\frac{2G(C-C_{12})}{C^2 - C_{12}C_{21}}, \frac{2G(C-C_{21})}{C^2 - C_{12}C_{21}}\right)$:

(x^*,y^*) is globally asymptotically stable when $C_{12} < C$ and $C_{21} < C$. Let us define $C_{12} = C - \alpha$ and $C_{21} = C - \alpha + \omega$, i.e. we firstly assume that $C_{21} < C_{12}$. To check if $a_{12} < 1$, we study the sign of $1 - a_{12}$, which can be calculated as a function $f(\alpha,\omega)$ as follows:

$$f(\alpha,\omega) = (C + \alpha)\omega^2 - 3\alpha^2\omega + 2\alpha^3,$$

Assuming a constant value of α, this is a second degree polynomial with respect to ω. The discriminant can be calculated and is $\Delta = \alpha(\alpha-8C)$, which is negative. Consequently, $1 - a_{12}$ is strictly positive. A similar result holds for a_{21}, i.e. $a_{21} < 1$. Thus, the aggregated competition model associated to this fast equilibrium point corresponds to a case of coexistence.

II.2 Equilibrium points $(\frac{2G}{C},0)$ and $(0,\frac{2G}{C})$:

when $C_{12}<C<C_{21}$, $(\frac{2G}{C},0)$ is g.a.s. When $C_{21} < C < C_{12}$ $(0,\frac{2G}{C})$ is g.a.s. and when $C_{12} > C$ and $C_{21} > C$, either $(\frac{2G}{C},0)$ or $(0,\frac{2G}{C})$ are asymptotically stable. A separatrix divides the domain into two parts corresponding to two basins of attraction.

Let us consider initial conditions inside the basin of attraction of $(\frac{2G}{C},0)$. To obtain the competition parameters of the aggregated model, let us substitute $(\frac{2G}{C},0)$ for $(\bar{x},\bar{y})$ in equation (12). An easy calculation leads to the following expressions:

$$a_{12} = 1-\frac{2G}{C}, \quad a_{21} = \frac{2G+C}{4G+C},$$

As we must have that $\frac{2G}{C} < 1$, it is obvious that $0 < a_{12}$ and $a_{21} < 1$, which corresponds to coexistence in Lotka-Volterra competition models. Consequently, for this fast equilibrium, the two populations globally coexist. The equilibrium populations $(\bar{n}_1, \bar{n}_2)$ are given by:

$$\bar{n}_1 = \bar{n}_2 = \frac{2\gamma C}{\delta(G+C)},$$

This equilibrium is lower than the equilibrium of each population alone. This is a general result of competition models. This is obvious because costs of fightings between individuals of the two populations have negative effects on the growth of each population.

The case of the point $(0,\frac{2G}{C})$ is identical to the previous one.

II.3 Equilibrium points $(x^*,y^*) = (0,1)$ and $(1,0)$:

Let us consider the fast equilibrium (0,1). To obtain the competition parameters of the aggregated model, let us substitute (0,1) for $(\bar{x},\bar{y})$ in equation (12). A simple calculation leads to the following expressions:

$$a_{12} = \frac{2G}{C+G}, \quad a_{21} = 0,$$

As a consequence, population 2 follows a logistic growth equation and tends to its carrying capacity. For population 1, two cases can occur:

- $C > G$: $a_{12} < 1$ and population 1 coexist.
- $C < G$: $a_{12} > 1$ and population 1 gets extinct.

A similar result holds for the fast equilibrium point (1,0).

ACKNOWLEDGMENTS

This work was supported by the grant DGCYT PB94 0396

REFERENCES

Auger, P. and R. Roussarie (1994). Complex ecological models with simple dynamics: From individuals to populations. Acta Biotheoretica 42: 111-113.

Auger, P. (1989). Dynamics and Thermodynamics in Hierarchically Organized Systems. Oxford, Pergamon Press.

Auger, P. and J.C. Poggiale (1995). Emerging properties in population dynamics with different time scales. J. Biological Systems 3: 591-602.

Auger, P. and J.C. Poggiale (1996). Emergence of population growth models: Fast migration and slow growth. J. Theor. Biol. in press.

Bravo de la Parra, R., P. Auger and E. Sanchez (1995). Aggregation methods in time discrete models. J. Biological Systems 3: 603-612.

Hofbauer, J. and K. Sigmund (1988). The Theory of Evolution and Dynamical Systems: Mathematical Aspects of Selection. Cambridge, Cambridge University Press.

Iwasa, Y., V. Andreasen and S.A. Levin (1987). Aggregation in model ecosystems I. Perfect aggregation. Ecol. Modelling 37: 287-302.

Iwasa, Y., S.A. Levin and V. Andreasen (1989). Aggregation in model ecosystems II. Approximate aggregation. IMA J. App. Med. Biol. 6: 1-23.

Maynard-Smith, J. (1982). Evolution and the Theory of Games. Cambridge, Cambridge University Press.

Sanchez, E., R. Bravo de la Parra and P. Auger (1995). Linear discrete models with different time scales. Acta Biotheoretica 43: 465-479.