BEHAVIORAL DYNAMICS OF TWO INTERACTING HAWK–DOVE POPULATIONS

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We present a model of two interacting populations using two individual strategies, hawk and dove. Individuals encounter each other frequently and can change tactics several times in their life. Conflicts occur between individuals belonging to the same population and to different populations. The general model is based on the replicator equations which are used to describe the variations of the hawk proportions of the two populations. According to parameter values, namely the gain-, the intra- and inter-population costs, and the relative intra-population encounter rates, we classify the different phase portraits. We show that a decrease in the intra-population cost of a population provokes an increase in the hawk proportion in this population and of the dove proportion in the other population. An increase in the inter-population cost favors hawk strategy in the population which causes more injuries and dove strategy in the other. We also study the effects of the relative densities of the two populations on the stability of equilibria. In most cases, an increase in the relative density of a population leads to a decrease in hawk proportion in this population and of dove proportion in the other.

1. Introduction

Evolutionary game theory started with pioneer works of J. Maynard Smith.[16] In this context, one considers a single population which is composed of individuals

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that can adopt different behavior strategies, either pure or mixed. The game is defined by the payoff matrix whose coefficients a_{ij} represent the benefit obtained by an individual playing strategy i against an individual playing strategy j. At any time, the population is divided into sub-populations of individuals playing the different strategies. The per capita growth rate of sub-population i is equal to the gain of an individual playing strategy i against the population.[9] A strategy that can resist invasion by any other strategy is said to be an Evolutionary Stable Strategy, ESS. Instead of choosing the numbers of individuals as variables, it is also frequent to consider the proportions (or frequencies) of individuals using the different tactics. The equations that govern the time evolution of the frequencies are referred to in the literature as the Replicator equations.[12] In these equations, one compares the gain of a given strategy, i.e. of an individual always playing this strategy against the population, to the average gain of individuals of the population. If this difference is positive, it is favorable to use this tactic and the proportion of individuals playing it is increasing. Otherwise, the corresponding sub-population is decaying. The replicator equations are a system of ODEs and an ESS corresponds to an equilibrium point of this system that must be at least locally asymptotically stable, l.a.s.. This condition l.a.s. is sufficient in the case of two strategies. In the general case of more than two possible strategies, it is required that the equilibrium point be strongly stable to be equivalent to an ESS.[8]

In the classical evolutionary game theory, an individual always adopts the same strategy during all its life. Individuals using strategies corresponding to large fitness better reproduce than others, leading in the long term to selection of the best fitted strategies. In some recent works,[1,3,18] it was assumed alternatively that individuals can adopt different tactics in their life. There is empirical evidence that the same individual can use different strategies in its life. Examples of behavior changing over time is widespread in mammals' taxa like, e.g., domestic cat *Felis catus*,[15] elephant seals *Mirounga angustirostris*,[11] red deer *Cervus elaphus*,[6] pronghorn *Antilocapra americana*[5] or gray squirrels *Sciurus carolinensis*.[14] In our approach an individual adopts the strategy that maximizes its benefit which is interpreted as a resource that individuals try to monopolize.

Game dynamics has been widely used to describe the behavioral dynamics of individuals belonging to a single population. In many concrete situations the population is not isolated but is interacting with at least another one. Individuals of both populations can compare different tactics taking into account encounters within their population and with individuals of the other one. In this case, it is necessary to weigh the influence of the different types of encounters. In general, one may assume that each population assigns any weight to every type of encounters. Two particular cases are of interest. Firstly, one can assume that the weights are equal which leads to the type of models for two interacting populations that are presented in Refs. 1, 9 and 18. A second case corresponds to a situation where the weights are equal to the relative proportions of the different types of encounters and thus depend on the relative densities of the two populations. This

work is based on a general model for the case of two populations and two tactics with weights that could be made explicit in any particular case. A close formulation can be found in Refs. 7 and 10.

In the classical hawk–dove game with a single population, when the cost C is larger than the gain G, the hawk proportion in the population tends to a constant G/C which is an ESS. At equilibrium, the population is polymorphic with constant proportions of hawks and doves. Otherwise, the population is pure hawk. In this paper, we shall consider the case of two populations and two tactics, hawk and dove. Consequently, two types of encounters can occur, intra-population encounters and inter-population ones. We assume that the gain G which corresponds to a common resource is identical for individuals of both populations. But, we assume that the costs due to fights between hawks are different within each population and between them. Thus, intra-population costs C_{11} and C_{22} and inter-populations ones C_{12} and C_{21} are defined. According to values of gain and costs, we shall find which combinations of tactics for both populations are compatible.

In Sec. 2, we present the general model for two populations and two tactics, hawk and dove. The mathematical model is based on the replicator equations.[12] In Sec. 3, we study the stability properties of the equilibrium points of this system. In Sec. 4, we classify the different phase portraits with respect to parameter values. In Sec. 5, we present two particular cases with different weights assigned to intra- and inter-population encounters. In Sec. 6, we study the effects of the relative population densities on the stability of the equilibria.

2. The Model

We consider a community of two populations whose individuals can use hawk (H) and dove (D) tactics. There are interactions between individuals of the same population and of different 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 of the two populations. The gains obtained by hawk and dove individuals of population i when interacting with hawk and dove individuals of population j are represented by matrix $\mathbf{A}_{ij}$ which is a classical hawk–dove matrix:

$$\mathbf{A}_{ij} = \begin{pmatrix} \dfrac{G - C_{ij}}{2} & G \\ 0 & \dfrac{G}{2} \end{pmatrix}. \tag{2.1}$$

Let $n_\alpha^{\mathrm{H}}(t)$ and $n_\alpha^{\mathrm{D}}(t)$ be respectively the numbers of individuals using hawk and dove strategies of population α, $\alpha = 1, 2$, at time t. The total population α is denoted $n_\alpha(t) = n_\alpha^{\mathrm{H}}(t) + n_\alpha^{\mathrm{D}}(t)$. Let $x_\alpha^{\mathrm{H}}(t)$ and $x_\alpha^{\mathrm{D}}(t)$ be the proportions of individuals using hawk and dove tactics:

$$x_\alpha^{\mathrm{H}} = \frac{n_\alpha^{\mathrm{H}}}{n_\alpha} \quad \text{and} \quad x_\alpha^{\mathrm{D}} = \frac{n_\alpha^{\mathrm{D}}}{n_\alpha}. \tag{2.2}$$

Let us denote $\mathbf{x}_1 = (x_1^{\mathrm{H}}, x_1^{\mathrm{D}})$ and $\mathbf{x}_2 = (x_2^{\mathrm{H}}, x_2^{\mathrm{D}})$.

Each individual compares the different tactics. An individual of population 1 using the pure H strategy against individuals of its own population sharing the two different tactics in proportions $\mathbf{x}_1$ gets the following payoff:

$$\Delta_{11}^{\mathrm{H}} = (1,0)\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}} \, ;$$

in this situation the average payoff of individuals of population 1 is:

$$\Delta_{11} = \mathbf{x}_1\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}} \, .$$

If population 1 was considered isolated, according to the classical replicator equations,[12] the proportion of individuals of population 1 using strategy H, x_1^{H}, would increase (resp. decrease) when its payoff would be larger (resp. smaller) than the average payoff of its population. As a consequence the relative rate of change of the proportion of hawks in population 1 would be proportional to the difference $\Delta_{11}^{\mathrm{H}} - \Delta_{11}$. In this work individuals of population 1 also encounter individuals of population 2. An individual of population 1 using the pure H strategy against individuals of population 2 sharing the two different tactics in proportions $\mathbf{x}_2$ gets the following payoff:

$$\Delta_{12}^{\mathrm{H}} = (1,0)\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}} \, ;$$

in this case the average payoff of individuals of population 1 is:

$$\Delta_{12} = \mathbf{x}_1\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}} \, .$$

If population 1 was only playing against population 2, the relative rate of change of the proportion of hawks in population 1 would be proportional to the difference $\Delta_{12}^{\mathrm{H}} - \Delta_{12}$.

In the case of coupled populations, that is when each individual encounters individuals of its own population and of the other one, it is necessary to consider at the same time the intra- and inter-population games weighted by a constant parameter representing the different influences of the two types of game. So the relative rate of change of the proportion of hawks in population 1 is assumed to be proportional to $\omega_1(\Delta_{11}^{\mathrm{H}} - \Delta_{11}) + (1 - \omega_1)(\Delta_{12}^{\mathrm{H}} - \Delta_{12})$, where ω_1 could be considered as the relative intra-population 1 encounter rate.

Extending the same reasoning to the proportions of hawk and dove in the two populations we can write the following set of ordinary differential equations which describes the change of H and D proportions in each population:

$$\begin{cases} \dfrac{dx_1^{\mathrm{H}}}{dt} = x_1^{\mathrm{H}}(\omega_1((1,0)\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}} - \mathbf{x}_1\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}}) + (1-\omega_1)((1,0)\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}} - \mathbf{x}_1\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}})) \, , \\[2mm] \dfrac{dx_1^{\mathrm{D}}}{dt} = x_1^{\mathrm{D}}(\omega_1((0,1)\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}} - \mathbf{x}_1\mathbf{A}_{11}\mathbf{x}_1^{\mathsf{T}}) + (1-\omega_1)((0,1)\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}} - \mathbf{x}_1\mathbf{A}_{12}\mathbf{x}_2^{\mathsf{T}})) \, , \\[2mm] \dfrac{dx_2^{\mathrm{H}}}{dt} = x_2^{\mathrm{H}}((1-\omega_2)((1,0)\mathbf{A}_{21}\mathbf{x}_1^{\mathsf{T}} - \mathbf{x}_2\mathbf{A}_{21}\mathbf{x}_1^{\mathsf{T}}) + \omega_2((1,0)\mathbf{A}_{22}\mathbf{x}_2^{\mathsf{T}} - \mathbf{x}_2\mathbf{A}_{22}\mathbf{x}_2^{\mathsf{T}})) \, , \\[2mm] \dfrac{dx_2^{\mathrm{D}}}{dt} = x_2^{\mathrm{D}}((1-\omega_2)((0,1)\mathbf{A}_{21}\mathbf{x}_1^{\mathsf{T}} - \mathbf{x}_2\mathbf{A}_{21}\mathbf{x}_1^{\mathsf{T}}) + \omega_2((0,1)\mathbf{A}_{22}\mathbf{x}_2^{\mathsf{T}} - \mathbf{x}_2\mathbf{A}_{22}\mathbf{x}_2^{\mathsf{T}})) \, . \end{cases} \tag{2.3}$$

If we call $\mathbf{A}$ the following matrix:

$$\mathbf{A} = \begin{pmatrix} \omega_1 \mathbf{A}_{11} & (1-\omega_1)\mathbf{A}_{12} \\ (1-\omega_2)\mathbf{A}_{21} & \omega_2 \mathbf{A}_{22} \end{pmatrix}, \tag{2.4}$$

after substitution of Eq. (2.1) we get

$$\mathbf{A} = \begin{pmatrix} \omega_1 \dfrac{G-C_{11}}{2} & \omega_1 G & (1-\omega_1)\dfrac{G-C_{12}}{2} & (1-\omega_1)G \\[2mm] 0 & \omega_1 \dfrac{G}{2} & 0 & (1-\omega_1)\dfrac{G}{2} \\[2mm] (1-\omega_2)\dfrac{G-C_{21}}{2} & (1-\omega_2)G & \omega_2 \dfrac{G-C_{22}}{2} & \omega_2 G \\[2mm] 0 & (1-\omega_2)\dfrac{G}{2} & 0 & \omega_2 \dfrac{G}{2} \end{pmatrix},$$

and we can write system (2.3) in a classical replicator form,[12,19] generalized to two populations,

$$\begin{cases} \dfrac{dx_1^{\mathrm{H}}}{dt} = x_1^{\mathrm{H}}((1,0,0,0)\mathbf{A}\mathbf{x}^{\mathsf{T}} - \mathbf{x}_1 \mathbf{A}\mathbf{x}^{\mathsf{T}}), \\[3mm] \dfrac{dx_1^{\mathrm{D}}}{dt} = x_1^{\mathrm{D}}((0,1,0,0)\mathbf{A}\mathbf{x}^{\mathsf{T}} - \mathbf{x}_1 \mathbf{A}\mathbf{x}^{\mathsf{T}}), \\[3mm] \dfrac{dx_2^{\mathrm{H}}}{dt} = x_2^{\mathrm{H}}((0,0,1,0)\mathbf{A}\mathbf{x}^{\mathsf{T}} - \mathbf{x}_2 \mathbf{A}\mathbf{x}^{\mathsf{T}}), \\[3mm] \dfrac{dx_2^{\mathrm{D}}}{dt} = x_2^{\mathrm{D}}((0,0,0,1)\mathbf{A}\mathbf{x}^{\mathsf{T}} - \mathbf{x}_2 \mathbf{A}\mathbf{x}^{\mathsf{T}}), \end{cases} \tag{2.5}$$

where $\mathbf{x}^{\mathsf{T}} = (x_1^{\mathrm{H}}, x_1^{\mathrm{D}}, x_2^{\mathrm{H}}, x_2^{\mathrm{D}})$.

Bearing in mind that $x_1^{\mathrm{H}} + x_1^{\mathrm{D}} = 1$ and $x_2^{\mathrm{H}} + x_2^{\mathrm{D}} = 1$, the previous system (2.5) reduces to the next two equations:

$$\begin{cases} \dfrac{dx}{dt} = \dfrac{1}{2}x(1-x)(G - \omega_1 C_{11} x - (1-\omega_1)C_{12} y), \\[3mm] \dfrac{dy}{dt} = \dfrac{1}{2}y(1-y)(G - (1-\omega_2)C_{21} x - \omega_2 C_{22} y), \end{cases} \tag{2.6}$$

where we denote $x = x_1^{\mathrm{H}}$ and $y = x_2^{\mathrm{H}}$, the proportions of hawk individuals in populations 1 and 2 respectively.

3. Stability of Equilibrium Points

System (2.6) is a set of two coupled ordinary differential equations. Our variables x and y vary in the interval [0,1]. Thus, the domain of study is the square $[0,1] \times [0,1]$. The steady states are located at its corners $(0,0)$, $(0,1)$, $(1,0)$, $(1,1)$, located on its boundaries,

$$\left(\frac{G}{\omega_1 C_{11}},0\right), \ \left(0,\frac{G}{\omega_2 C_{22}}\right), \ \left(1,\frac{G-(1-\omega_2)C_{21}}{\omega_2 C_{22}}\right), \ \left(\frac{G-(1-\omega_1)C_{12}}{\omega_1 C_{11}},1\right),$$

and one point

$$Q = (x^*, y^*)$$

$$= \left(\frac{G(\omega_2 C_{22}-(1-\omega_1)C_{12})}{\omega_1\omega_2 C_{11}C_{22}-(1-\omega_1)(1-\omega_2)C_{12}C_{21}}, \ \frac{G(\omega_1 C_{11}-(1-\omega_2)C_{21})}{\omega_1\omega_2 C_{11}C_{22}-(1-\omega_1)(1-\omega_2)C_{12}C_{21}}\right)$$

inside the domain (according to parameter values). The lines $x=0$, $x=1$, $y=0$ and $y=1$ are nullclines. Consequently, the square $[0,1]\times[0,1]$ is invariant and the ω-limit set of every orbit inside the square is an equilibrium point of this domain because the system is competitive.

The Jacobian matrix associated to system (2.6) reads as follows:

$$J(x,y) =$$
$$\begin{pmatrix} \frac{1}{2}(1-2x)(G-\omega_1 C_{11}x-(1-\omega_1)C_{12}y)-\frac{1}{2}\omega_1 C_{11}x(1-x) & -\frac{1}{2}(1-\omega_1)C_{12}x(1-x) \\ -\frac{1}{2}(1-\omega_2)C_{21}y(1-y) & \frac{1}{2}(1-2y)(G-\omega_2 C_{22}y-(1-\omega_2)C_{21}x)-\frac{1}{2}\omega_2 C_{22}y(1-y) \end{pmatrix}.$$

We can obtain the following conditions (details of the calculation are given in the appendix) for the local asymptotic stability (l.a.s.) of equilibrium points:

$(0,0)$ never l.a.s. .

$(0,1)$ l.a.s. if $\omega_2 C_{22} < G < (1-\omega_1)C_{12}$.

$(1,0)$ l.a.s. if $\omega_1 C_{11} < G < (1-\omega_2)C_{21}$.

$(1,1)$ l.a.s. if $\max\{\omega_1 C_{11}+(1-\omega_1)C_{12}, \omega_2 C_{22}+(1-\omega_2)C_{21}\} < G$.

$\left(\dfrac{G}{\omega_1 C_{11}},0\right)$ l.a.s. if $G < \omega_1 C_{11} < (1-\omega_2)C_{21}$,

$\left(0,\dfrac{G}{\omega_2 C_{22}}\right)$ l.a.s. if $G < \omega_2 C_{22} < (1-\omega_1)C_{12}$,

$\left(1,\dfrac{G-(1-\omega_2)C_{21}}{\omega_2 C_{22}}\right)$ l.a.s. if $0 < G-(1-\omega_2)C_{21} < \omega_2 C_{22}$ and

   $G(\omega_2 C_{22}-(1-\omega_1)C_{12}) > \omega_1\omega_2 C_{11}C_{22}-(1-\omega_1)(1-\omega_2)C_{12}C_{21}$,

$\left(\dfrac{G-(1-\omega_1)C_{12}}{\omega_1 C_{11}},1\right)$ l.a.s. if $0 < G-(1-\omega_1)C_{12} < \omega_1 C_{11}$ and

   $G(\omega_1 C_{11}-(1-\omega_2)C_{21}) > \omega_1\omega_2 C_{11}C_{22}-(1-\omega_1)(1-\omega_2)C_{12}C_{21}$,

$Q = (x^*, y^*)$ l.a.s. if $\omega_1\omega_2 C_{11}C_{22} > (1-\omega_1)(1-\omega_2)C_{12}C_{21}$,

   $0 < x^* < 1$ and $0 < y^* < 1$.

4. Phase Portraits

In Sec. 3, we studied the local stability properties of equilibrium points. In this section, we shall describe the phase portraits corresponding to the different set of values of the parameters. To simplify the notations, let us define the following parameters:

$$\alpha = \frac{G}{\omega_1 C_{11}}, \; \beta = \frac{G - (1 - \omega_1)C_{12}}{\omega_1 C_{11}}, \gamma = \frac{G - (1 - \omega_2)C_{21}}{\omega_2 C_{22}} \text{ and } \delta = \frac{G}{\omega_2 C_{22}}, \quad (4.1)$$

which correspond to the locations of the equilibrium points on the lines $x = 0$, $x = 1$, $y = 0$ and $y = 1$. The parameter $\alpha = \frac{G}{\omega_1 C_{11}}$ ($\delta = \frac{G}{\omega_2 C_{22}}$) is proportional to the fraction of aggressive individuals in population 1 (2) when uncoupled to population 2 (1). Indeed, in the classical hawk–dove game, when $G < C$, the equilibrium proportion of hawks is equal to G/C. If population 1 is isolated, i.e. uncoupled to population 2, the equilibrium proportion of hawks would be $G/C_{11} = \omega_1 \alpha$. It represents the initial (or potential) hawk proportion of population 1. A similar result holds for population 2 with a potential hawk proportion $G/C_{22} = \omega_2 \delta$. If α is close to zero, individuals of population 1 if isolated from 2 would be mainly dove. If δ is close to $1/\omega_2$, individuals of uncoupled population 2 would be mostly hawks. Thus, α and δ are directly related to the potential aggressiveness of individuals in both populations before coupling.

The parameters of the model are linked by the following relations, $\beta = \alpha - \frac{(1-\omega_1)C_{12}}{\omega_1 C_{11}}$ and $\gamma = \delta - \frac{(1-\omega_2)C_{21}}{\omega_2 C_{22}}$. While parameters α and δ are positive, parameters β and γ can be positive, negative or even equal to zero. Furthermore, β and γ must remain respectively smaller than α and δ which determine some possible domains for the parameters. An increase in the inter-population costs (C_{12}, C_{21}) corresponding to fighting between individuals belonging to different populations leads to a decrease in the parameter values, β and γ.

The phase portraits depend on the relative positions of the two following lines (nullclines) R_1 and R_2 with respect to the unit square:

$$\begin{aligned} R_1 &: G - \omega_1 C_{11}x - (1 - \omega_1)C_{12}y = 0, \\ R_2 &: G - \omega_2 C_{22}y - (1 - \omega_2)C_{21}x = 0, \end{aligned} \quad (4.2)$$

which are respectively x and y-nullclines. In Fig. 1, we distinguish five different positions of the x-nullcline R_1 corresponding to five cases noted as I, II, III, IV and V. Figure 2 presents the domains which are associated to these five regions with respect to parameters α and β. As we have seen earlier, the domain of interest for the parameter plane (α, β) corresponds to $\alpha > 0$ and to $\beta < \alpha$. This possible domain is divided into the five sub-domains of Fig. 1 that we still note in the same way I, II, III, IV and V.

In each of these cases, one still must distinguish five positions of the nullcline R_2 which we note as i, ii, iii, iv and v, see Fig. 3. The combination of the two relative positions of R_1 and R_2 nullclines leads to different cases that we shall now study.
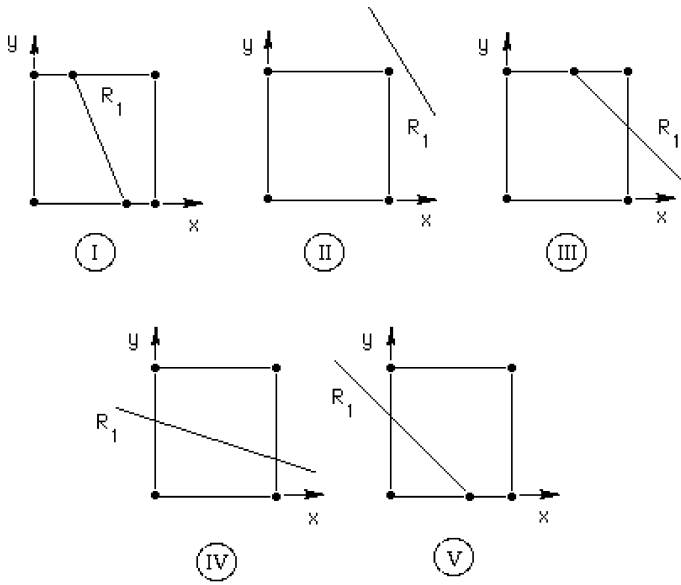
Fig. 1.   The different positions that the nullcline R_1 can take corresponding to five different cases I, II, III, IV and V.
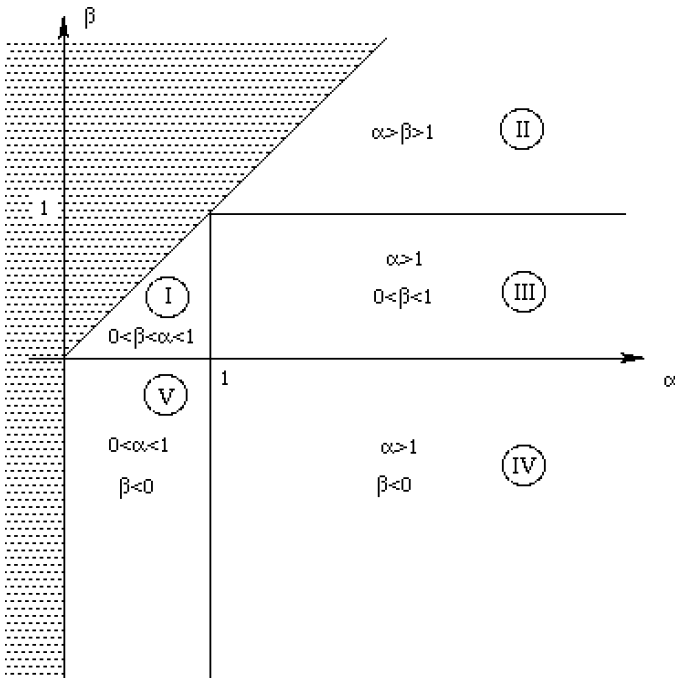

Fig. 2.   The five different cases I, II, III, IV and V of Fig. 1 represented in the parameter plane (α, β).
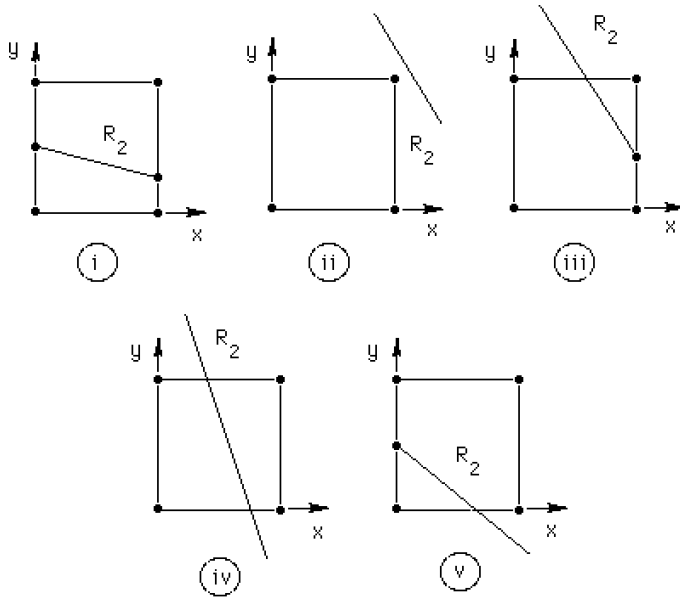
Fig. 3.   The different positions that the nullcline R_2 can take corresponding to five different cases i, ii, iii, iv and v.
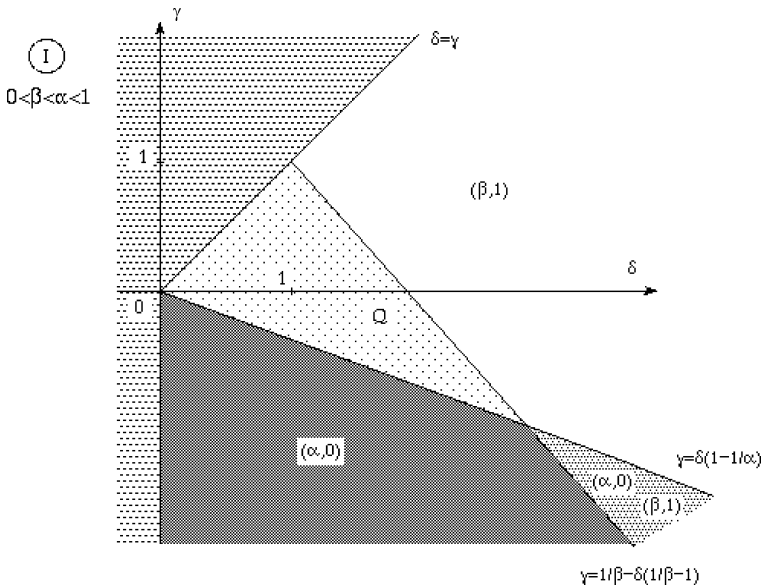

Fig. 4.   Case I, $\frac{G}{\omega_1 C_{11}} < 1$, initial mixed population 1, $G < \omega_1 C_{11} + (1 - \omega_1)C_{12}$ and $G > (1 - \omega_1)C_{12}$. Different possible ω-limit sets according to sub-domains of the parameter plane (δ, γ). In the region noted $(\alpha, 0)$, all orbits within the unit square tends to the asymptotically stable equilibrium $(\alpha, 0)$. In the region noted $(\alpha, 0)$ and $(\beta, 1)$, according to the initial condition within the unit square , either the trajectory tends to the asymptotically stable point $(\alpha, 0)$ or to $(\beta, 1)$.
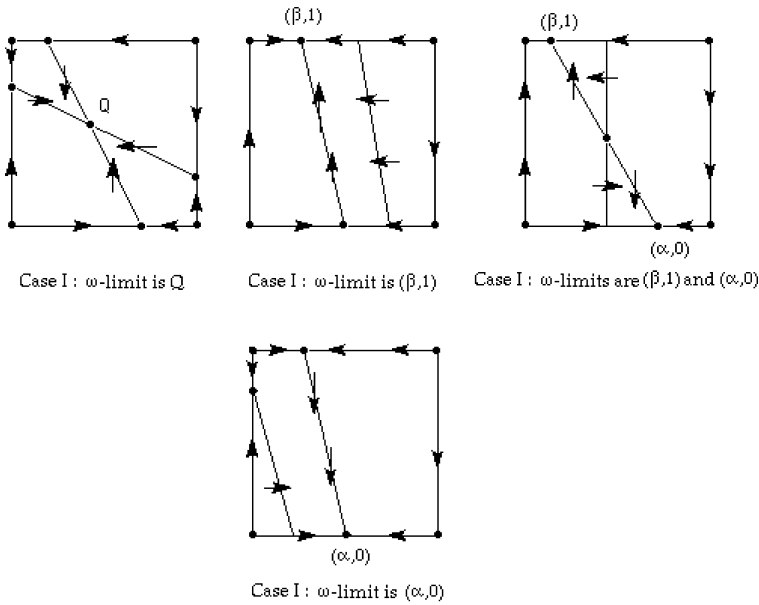
Fig. 5.   Case I, different phase portraits that correspond to the different possibilities shown in Fig. 4.

We shall classify the phase portraits corresponding to each case I, II, III, IV and V. Case I corresponds to a domain in the (α, β) plane of Fig. 2. Figure 4 shows the possible ω-limits of case I according to different values of the parameters δ and γ. As for the (α, β) plane, the domain of interest for the parameter plane (δ, γ) corresponds to $\delta > 0$ and $\gamma < \delta$. The (δ, γ) plane is divided into regions where the equilibrium points that are asymptotically stable are indicated. When a single equilibrium point is indicated, it is globally asymptotically stable in the unit square. When two equilibrium points are noted, both are asymptotically stable and there exists a separatrix which is the boundary of their domains of attraction. Figure 5 shows examples of phase portraits associated to each of the (δ, γ) sub-domains of Fig. 4. Figures 6–9 show the possible ω-limits of cases II, III, IV and V respectively.

Given gain G, costs C_{11}, C_{22}, C_{12} and C_{21}, and relative intra-population encounter rates ω_1 and ω_2, the values of the parameters α, β, γ and δ are fixed. Therefore, it is possible by use of the previous figures to check easily which equilibrium points are stable in each particular case.

Common trends are found in Figs. 4 and 6 to 9. When parameter δ is fixed, an increase in parameter γ corresponds to an increase in the hawk proportion in population 2. For example, in Fig. 6, case II, a vertical line in the direction of increasing γ values corresponds to a hawk proportion of population 2 varying from 0 to 1. When fixing a δ value, the potential hawk proportion within population 2 is chosen. Then, an increase in parameter γ corresponds to a decrease in inter-cost C_{21}. This means that injuries caused by individuals of population 1 to individuals
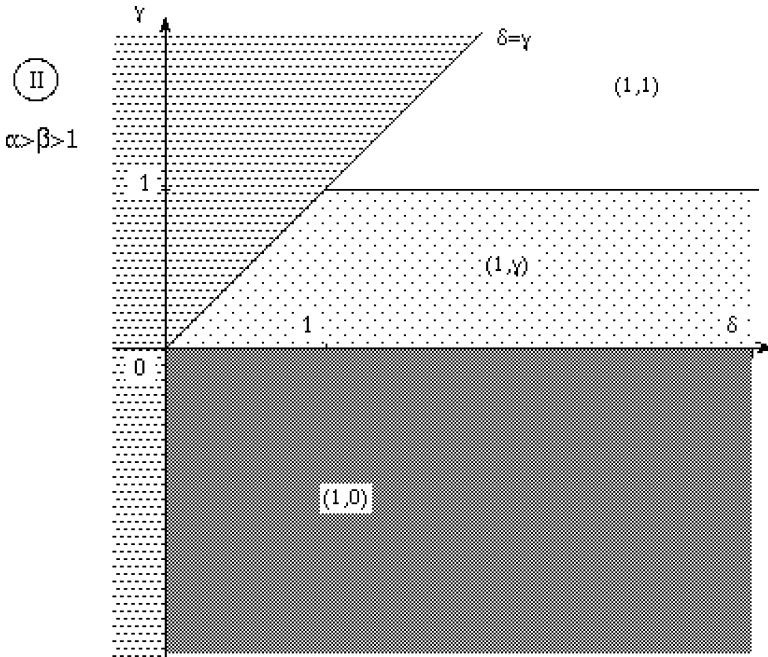
Fig. 6. Case II, $\frac{G}{\omega_1 C_{11}} > 1$, initial hawk population 1. $G > \omega_1 C_{11} + (1 - \omega_1)C_{12}$. Different possible ω-limit sets according to sub-domains of the parameter plane (δ, γ).
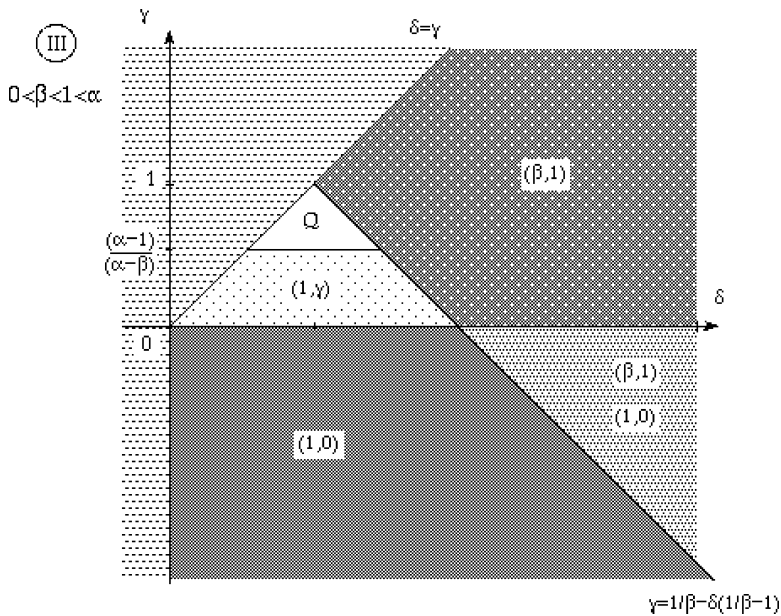

Fig. 7. Case III, $\frac{G}{\omega_1 C_{11}} > 1$, initial hawk population 1. $(1 - \omega_1)C_{12} < G < \omega_1 C_{11} + (1 - \omega_1)C_{12}$. Different possible ω-limit sets according to sub-domains of the parameter plane (δ, γ).
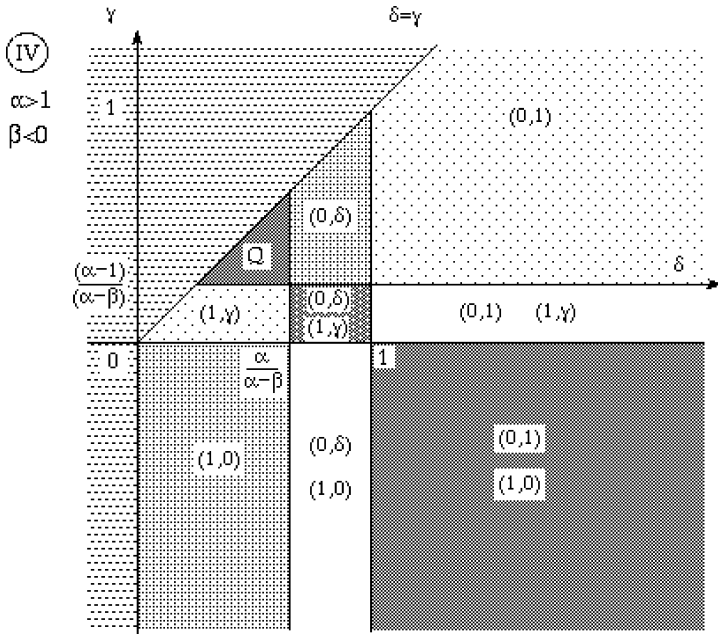
Fig. 8.   Case IV, $\frac{G}{\omega_1 C_{11}} > 1$, initial hawk population 1. $\omega_1 C_{11} < G < (1 - \omega_1)C_{12}$. Different possible ω-limit sets according to sub-domains of the parameter plane (δ, γ).
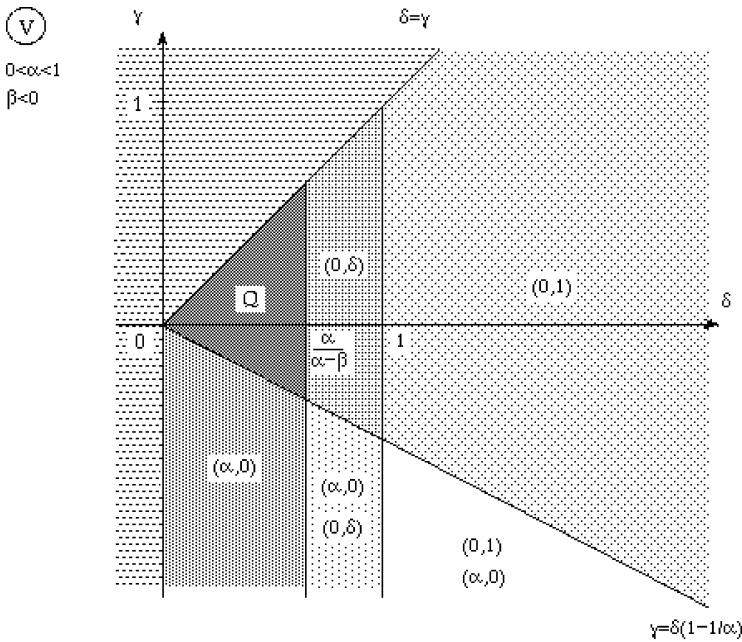

Fig. 9.   Case V, $\frac{G}{\omega_1 C_{11}} < 1$, initial mixed population 1. $(1 - \omega_1)C_{12} < G < \omega_1 C_{11}$. Different possible ω-limit sets according to sub-domains of the parameter plane (δ, γ).

of population 2 are weaker. In turn, this favors the hawk strategy in population 2. On the other hand, an increase in parameter γ also corresponds to a decrease in the hawk proportion in population 1. For example in Fig. 8 case IV, a vertical line can change the hawk proportion of population 1 from 1 to 0. Indeed, a decrease in the inter-cost C_{21} means that individuals of population 1 cause fewer injuries when they fight against individuals of population 2. Consequently, the hawk proportion in population 1 decreases.

In all cases I–V, we can also see that a horizontal line in the direction of increasing δ values corresponds to an increase in the hawk proportion in population 2 and a decrease in the hawk proportion in population 1. Indeed, when inter-population cost C_{21} is fixed, an increase in δ corresponds to an increase in the potential proportion of hawks in population 2. This in turn causes a decrease in the hawk proportion of the other opponent population 1 because its individuals encounter more and more aggressive individuals of population 2. It also favors an increase in hawks in population 2 which become more efficient against individuals of population 1.

To summarize:

– An increase in the inter population costs always favors hawk strategy in the population which causes more injuries and dove strategy in the other.
– An increase in the potential hawk proportion in a population (before coupling), favors hawk strategy in this population and dove strategy in the other (after coupling).

5. Some Particular Cases of Relative Intra-Population Encounter Rates

Assuming that intra- and inter-population encounters are similarly weighted we must choose $\omega_1 = \omega_2 = 1/2$. Such an assumption is implicit in Sec. 3 of the book by Cressman.[9] In that case, system (2.6) reads:

$$\begin{cases} \dfrac{dx}{dt} = \dfrac{1}{4}x(1-x)(2G - C_{11}x - C_{12}y)\,, \\[2mm] \dfrac{dy}{dt} = \dfrac{1}{4}y(1-y)(2G - C_{21}x - C_{22}y)\,. \end{cases} \qquad (5.1)$$

In other cases, it is necessary to take into account the densities n_1 and n_2. For instance, if we have many individuals in population 1 (large n_1) and few individuals in population 2 (small n_2), individuals of population 2 will mostly encounter individuals of population 1. This density effect was not considered in model (5.1). In order to consider this density effect, we must choose $\omega_1 = n_1/n$ and $\omega_2 = n_2/n$, where $n = n_1 + n_2$.

This leads us to consider the next set of differential equations:

$$\begin{cases} \dfrac{dx}{dt} = \dfrac{x}{2n}(1-x)(G(n_1 + n_2) - C_{11}n_1x - C_{12}n_2y)\,, \\[2mm] \dfrac{dy}{dt} = \dfrac{y}{2n}(1-y)(G(n_1 + n_2) - C_{21}n_1x - C_{22}n_2y)\,. \end{cases} \qquad (5.2)$$

In this system population densities (n_1, n_2) are constant parameters.

Another way to derive system (5.2) is to consider a new system whose variables are densities $(n_1^H, n_1^D, n_2^H, n_2^D)$:

$$
\begin{cases}
\dfrac{dn_1^H}{dt} = \dfrac{n_1^H}{nn_1}\left((n_1, 0, 0, 0)\mathbf{An}^\mathsf{T} - \mathbf{n}_1\mathbf{An}^\mathsf{T}\right), \\[2mm]
\dfrac{dn_1^D}{dt} = \dfrac{n_1^D}{nn_1}\left((0, n_1, 0, 0)\mathbf{An}^\mathsf{T} - \mathbf{n}_1\mathbf{An}^\mathsf{T}\right), \\[2mm]
\dfrac{dn_2^H}{dt} = \dfrac{n_2^H}{nn_2}\left((0, 0, n_2, 0)\mathbf{An}^\mathsf{T} - \mathbf{n}_2\mathbf{An}^\mathsf{T}\right), \\[2mm]
\dfrac{dn_2^D}{dt} = \dfrac{n_2^D}{nn_2}\left((0, 0, 0, n_2)\mathbf{An}^\mathsf{T} - \mathbf{n}_2\mathbf{An}^\mathsf{T}\right),
\end{cases}
\tag{5.3}
$$

where we have used the following notations: $\mathbf{n} = (n_1^H, n_1^D, n_2^H, n_2^D)$, $\mathbf{n}_1 = (n_1^H, n_1^D, 0, 0)$ and $\mathbf{n}_2 = (0, 0, n_2^H, n_2^D)$.

One must note that n_1 and n_2 are constants of motion for Eq. (5.3) and thus are constant parameters.

6. Density Effects on Game Dynamics

In the cases when both populations are monomorphic at equilibrium the relative densities (ω_1, ω_2) only affect the size of the parameters domain in which the steady state is l.a.s.

In the cases when at least one of the populations is mixed at equilibrium the hawk proportion depends on relative densities:

- $(\frac{G}{\omega_1 C_{11}}, 0)$. The hawk proportion of population 1 is a decreasing function of ω_1. This means that population 1, which is encountering a completely dove population 2, is becoming less aggressive as its relative density increases.
- $(0, \frac{G}{\omega_2 C_{22}})$. This is the symmetric case to the previous one.
- $(1, \frac{G-(1-\omega_2)C_{21}}{\omega_2 C_{22}})$. If $G > C_{21}$ the hawk proportion of population 2 is a decreasing function of ω_2. This result is similar to the previous cases. If $G < C_{21}$ we find the opposite relationship. In that case population 2 encounters a pure hawk population 1 which causes important injuries to it — an increase in the relative density of population 2 yields an increase in its hawk proportion.
- $(\frac{G-(1-\omega_1)C_{12}}{\omega_1 C_{11}}, 1)$. Analogous to the previous one.
- $Q = (x^*, y^*) = (\frac{G(C_{22}-C_{12})}{C_{11}C_{22}-C_{12}C_{21}}\frac{1}{\omega_1}, \frac{G(C_{11}-C_{21})}{C_{11}C_{22}-C_{12}C_{21}}\frac{1}{\omega_2})$. In this case the increase in the relative proportion of any of the two populations provokes a decrease in its hawk proportion.

To summarize we have found that in most cases an increase in relative density of a population leads to a decrease in its hawk proportion.

7. Discussion and Conclusion

In this paper, we have classified the different phase portraits for two interacting hawk–dove populations. There are many possibilities because pure as well as mixed equilibria are possible for both populations. Furthermore, several equilibria can be stable at the same time. However, it was possible to find general common trends that we now summarize: An increase in the potential aggressiveness of a population favors a mixed strategy with a high hawk proportion in this population and dove proportion in the other. An increase in injuries caused by a population to another provokes an increase in hawk proportion in the first population and of dove proportion in the second one.

In this contribution, population densities are constant. But, in Sec. 6 we have studied the effects of the relative densities of the populations on equilibria. We found that in most cases, an increase in the relative proportion of a population favors the increase in hawk proportion in this population and of dove proportion in the other.

In Ref. 3, we considered a single population with hawk and dove individuals. We considered two time scales, a fast one for the game dynamics and a slow one for the demography of the population. We used aggregation methods to obtain an equation governing the total population at the slow time scale. Aggregation methods are based on different time scales and allow us to reduce the dimension of the dynamical system.[2,4,13,17] This reduced model was a logistic equation with a carrying capacity that was a decreasing function of the hawk proportion of the population at the fast equilibrium. This leads us to the following interpretation: Large populations in urban areas are mainly dove while small density populations in rural areas are aggressive. This result was confirmed by empirical evidence in the case of domestic cat populations.

In this paper, the densities of the two populations are constant parameters. In a future work, we shall couple the present game dynamics model for two populations and two tactics with a population dynamics model. To perform this, we shall assume that the game dynamics corresponds to a fast time scale with respect to demography. Therefore, we shall use this new model to study the influence of the individual behavior selected by individuals of both populations (hawk or dove) at the fast time scale on their coexistence or mutual exclusion in the long term. This will allow us to study the coevolution of the behavioral dynamics and of the population dynamics. This aspect was partly discussed in Sec. 6 of this paper as equilibrium points depend on the relative population densities. But, the next step is to connect the two types of models, game and population dynamics and to study the coupling between both processes, i.e. the effects of densities on the tactics adopted by individuals but also the effects of strategies selected by individuals on the dynamics of their population densities.

Appendix. Local Stability Analysis of the Equilibrium Points

In the case of the origin the Jacobian matrix reads:

$$J(0,0) = \begin{pmatrix} G & 0 \\ 0 & G \end{pmatrix}.$$

The two eigenvalues are equal to the positive parameter G and the origin is an unstable node.

In the case of the $(1, 0)$ the Jacobian matrix reads:

$$J(1,0) = \begin{pmatrix} -\dfrac{1}{2}(G - \omega_1 C_{11}) & 0 \\ 0 & \dfrac{1}{2}(G - (1 - \omega_2)C_{21}) \end{pmatrix}.$$

Thus, $(1, 0)$ is a stable node if both entries on the main diagonal are negative which can be expressed by $\omega_1 C_{11} < G < (1 - \omega_2)C_{21}$. A similar result holds for the equilibrium points $(0, 1)$ and $(1, 1)$ which have a diagonal Jacobian matrix.

In the case of the equilibrium point $(\frac{G}{\omega_1 C_{11}}, 0)$ the Jacobian matrix reads:

$$J\left(\frac{G}{\omega_1 C_{11}}, 0\right) = \begin{pmatrix} G\left(\dfrac{G}{\omega_1 C_{11}} - 1\right) & G\dfrac{(1 - \omega_1)C_{12}}{\omega_1 C_{11}}\left(\dfrac{G}{\omega_1 C_{11}} - 1\right) \\ 0 & G\left(1 - \dfrac{(1 - \omega_2)C_{21}}{\omega_1 C_{11}}\right) \end{pmatrix}.$$

As the matrix is triangular, the eigenvalues are the entries of the main diagonal. Thus, the equilibrium point is a stable node if both eigenvalues are negative which can be expressed by $G < \omega_1 C_{11} < (1 - \omega_2)C_{21}$. In the case of the three equilibrium points $(0, \frac{G}{\omega_2 C_{22}})$, $(1, \frac{G - (1 - \omega_2)C_{21}}{\omega_2 C_{22}})$ and $(\frac{G - (1 - \omega_1)C_{12}}{\omega_1 C_{11}}, 1)$, the Jacobian matrix is also triangular and the stability conditions are easily found.

In the remaining case of the equilibrium point $Q = (x^*, y^*)$, after some algebra, the Jacobian matrix reads:

$$J(x^*, y^*) = \begin{pmatrix} -\dfrac{\omega_1 C_{11}}{2}x^*(1 - x^*) & -\dfrac{(1 - \omega_1)C_{12}}{2}x^*(1 - x^*) \\ -\dfrac{(1 - \omega_2)C_{21}}{2}y^*(1 - y^*) & -\dfrac{\omega_2 C_{22}}{2}y^*(1 - y^*) \end{pmatrix}.$$

The equilibrium point $Q = (x^*, y^*)$ must be located inside the unit square to make sense, i.e. $0 < x^* < 1$ and $0 < y^* < 1$. Then, the trace of the Jacobian matrix is negative. To be a sink, its determinant must be positive leading to the condition $\omega_1 C_{11} \omega_2 C_{22} - (1 - \omega_1)C_{12}(1 - \omega_2)C_{21} > 0$.

Acknowledgment

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