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Hawk-Dove Game and Competition Dynamics

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Abstract—In this article, we consider two populations subdivided into two categories of individuals (hawks and doves). Individuals fight to have access to a resource necessary for their growth. Conflicts occur between hawks of the same population and hawks of different populations. The aim of this work is to investigate the long term effects of these conflicts on coexistence and stability of the community of the two populations. This model involves four variables corresponding to the two tactics of individuals of the two populations. The model is composed of two parts, a fast part describing the encounters and fights, and the slow part describing the long term effects of encounters on the growth of the populations. We use aggregation methods allowing us to reduce this model into a system of two ODEs for the total densities of the two populations. This is found to be a classical Lotka-Volterra competition model. We study the effects of the different fast equilibrium proportions of hawks and doves in both populations on the global coexistence and the mutual exclusion of the two populations. We show that in some cases, mixed hawk and dove populations coexist. Aggressive populations of hawks exclude doves except in the case of interpopulation costs being smaller than intrapopulation ones.

Keywords—Individual conflicts, Access to resources, Two populations, Hawk and dove tactics, Coexistence, Exclusion.

1. INTRODUCTION

An important aspect of population dynamics is the study of the effects of different individual strategies on the stability of the population and of the community. In this work, we assume a community of two populations. Individuals of both populations compete for a given resource which is necessary for their growth. This important resource is scarce so that individuals have to fight to have access to the resource. We have chosen classical hawk and dove tactics [1,2]. The hawk is aggressive and fights in any case. The dove never fights. When a hawk meets a dove, he is the winner. When two hawks meet, they fight, inducing injuries which may cause the death of one of them. When two doves meet, they do not fight; one of them leaves and the other one has access to the food.

In this article, we consider two populations each one being composed of hawks and doves. Hawks and doves not only play against individuals of their population but, also against individuals of the other one. Thus, we consider a payoff matrix with dimension four. The winner gets the gain G which is assumed similar for all individuals because it corresponds to an access to the resource. Intrapopulation costs C due to hawk-hawk conflicts are similar for both populations.

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But, the asymmetry comes from the interpopulation costs C_{12} and C_{21} which are different. For example, if $C_{12} > C_{21}$, this means that hawks of population 2 can provoke more important injuries to hawks of population 1 than the reverse. The aim of this paper is to investigate under which particular conditions the two populations will coexist or mutually exclude each other.

To perform this goal, we consider two time scales. A fast time scale at which individuals play the hawk-dove game. Individuals must feed every day. Thus, they need to have access to the resource frequently. There is also a slow time scale at which the growth of the total density of the populations is considered. Consequently, our model is composed of two parts, a fast part describing the intrapopulation and interpopulation game dynamics and a slow describing the long term effects of hawk and dove encounters on the growth of the populations.

This model is composed of our four slow-fast ordinary differential equations governing the variables associated to hawk and dove subpopulations belonging to the two populations. We use aggregation methods to reduce the dimension to two equations for the total densities of populations 1 and 2, [3,4]. This aggregated slow model is found to be a classical Lotka-Volterra competition model. Consequently, populations can coexist or exclude each other. We study the effects of different proportions of hawks and doves at the fast equilibrium on the coexistence or exclusion of both populations in the long term. We have not studied all possibilities (which are large) because one can make combinations of the different equilibria of the fast system with the different equilibria of the slow one. Our result shows that both coexistence and exclusion can occur. Exclusion occurs when all individuals are hawks in both populations.

2. THE GENERAL MODEL

We consider a system of two populations each one 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 change tactics from one encounter to the next, at a fast time scale. 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 strategies and the slow part which describes the long-term effects of the conflicts on the growth of the subpopulations.

2.1. Fast Part: Game Dynamics

As the winner of the 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 classical H-D game matrix A

$$A = \begin{pmatrix} \dfrac{G-C}{2} & G & \dfrac{G-C_{12}}{2} & G \\ 0 & \dfrac{G}{2} & 0 & \dfrac{G}{2} \\ \dfrac{G-C_{21}}{2} & G & \dfrac{G-C}{2} & G \\ 0 & \dfrac{G}{2} & 0 & \dfrac{G}{2} \end{pmatrix}. \tag{1}$$

We also assume that the costs C due to injuries of hawks conflicts are identical within both populations. However, the asymmetry comes from different costs when a hawk encounters another hawk of the other population. Let C_{12} (respectively, C_{21}) be the cost when a hawk of population 1 (respectively, 2) fights against a hawk of population 2 (respectively, 1). Let n_α^H and n_α^D be, respectively, the hawks and doves subpopulations 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 (respectively, x_2^H and x_2^D) be the proportions of hawk and dove in the total population 1 (respectively, 2):

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

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

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

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

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

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

Each individual changes tactics at a fast time-scale and thus compares the different tactics in his life. System (3) describes the dynamics of the proportions of individuals using the different strategies. These equations are classical replicator equations (see [1]). The proportion of individuals of population 1 playing H, i.e., x_1^H, increases when the payoff of an individual always using strategy H is better than the average payoff of an individual of its population, i.e., playing H in proportion x_1^H and D in proportion x_1^D against a population sharing the different tactics in proportions $(x_1^H, x_1^D, x_2^H, x_2^D)$.

One must note that $x_1^H + x_1^D = 1$ and $x_2^H + x_2^D = 1$. Consequently, the previous 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 Subpopulations

For each subpopulation (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 subpopulation is thus described as follows:

$$\frac{dn_1^H}{dt} = rn_1^H - k_{11}^H n_1^H n_1^H - k_{11}^{HD} n_1^H n_1^D - k_{12}^H n_1^H n_2^H - k_{12}^{HD} n_1^H n_2^D, \tag{5a}$$

$$\frac{dn_1^D}{dt} = rn_1^D - k_{11}^{DH} n_1^D n_1^H - k_{11}^D n_1^D n_1^D - k_{12}^{DH} n_1^D n_2^H - k_{12}^D n_1^D n_2^D, \tag{5b}$$

$$\frac{dn_2^H}{dt} = rn_2^H - k_{21}^H n_2^H n_1^H - k_{21}^{HD} n_2^H n_1^D - k_{22}^H n_2^H n_2^H - k_{22}^{HD} n_2^H n_2^D, \tag{5c}$$

$$\frac{dn_2^D}{dt} = rn_2^D - k_{21}^{DH} n_2^D n_1^H - k_{21}^D n_2^D n_1^D - k_{22}^{DH} n_2^D n_2^H - k_{22}^D n_2^D n_2^D. \tag{5d}$$

Here, r is the linear growth rate assumed to be identical for all the subpopulations. The quadratic terms take into account the negative effects of encounters between individuals in the same population and between different populations. The growth rate r is defined as

$$r = 2\gamma G,$$

where this equation means that the growth rate is assumed to be proportional to the gain G. γ is a positive constant which represents a conversion coefficient of the gain G of the resource into biomass of the individual.

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_{ij} are the entries of the payoff matrix A and δ is a 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 matrix coefficients into the previous expressions leads to

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

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

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

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

2.3. The Complete Model

The complete model is obtained by coupling the two parts presented above

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

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

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

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

where ε is a small parameter. It must be noted that the fast systems are conservative, i.e., the total populations n_1 and n_2 are constants of motion. The complete system is then obtained by substitution of expressions (6) into system (7).

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 located on its corners (0,0), (0,1), (1,0), (1,1), located on its boundaries, $((2G/C), 0)$, $(0, (2G/C))$, $(1, (2G - C_{21})/C)$, $((2G - C_{12})/C, 1)$, and one point

$$\left(\frac{(2G - C_{12})}{C^2 - C_{12}C_{21}}, \frac{(2G - C_{21})}{C^2 - C_{12}C_{21}}\right) = (x^*, y^*),$$

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 A:

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

where $r = 2\gamma G$ and we have the following expressions:

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

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

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

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. AGGRESSIVENESS IN RELATIONSHIP TO COEXISTENCE AND EXCLUSION

4.1. The Case of Hawks and Doves Mixed Populations

In this section, we make the restriction of the study to the case $2G/C < 1$.

$x = 0$, $x = 1$, $y = 0$, 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. One can distinguish the following four cases.

(a) $C_{12} < C$ and $C_{21} < C$: (x^*, y^*) is globally asymptotically stable, g.a.s. This means that for any initial condition in $]0,1[\times]0,1[$, the trajectory tends to (x^*, y^*).
(b) $C_{12} < C < C_{21}$: $((2G/C), 0)$ is g.a.s.
(c) $C_{21} < C < C_{12}$: $(0, (2G/C))$ is g.a.s.
(d) $C_{12} < C$ and $C_{21} > C$: $((2G/C), 0)$, and $(0, (2G/C))$ are asymptotically stable. A separatrix divides the domain into two parts corresponding to two basins of attraction.

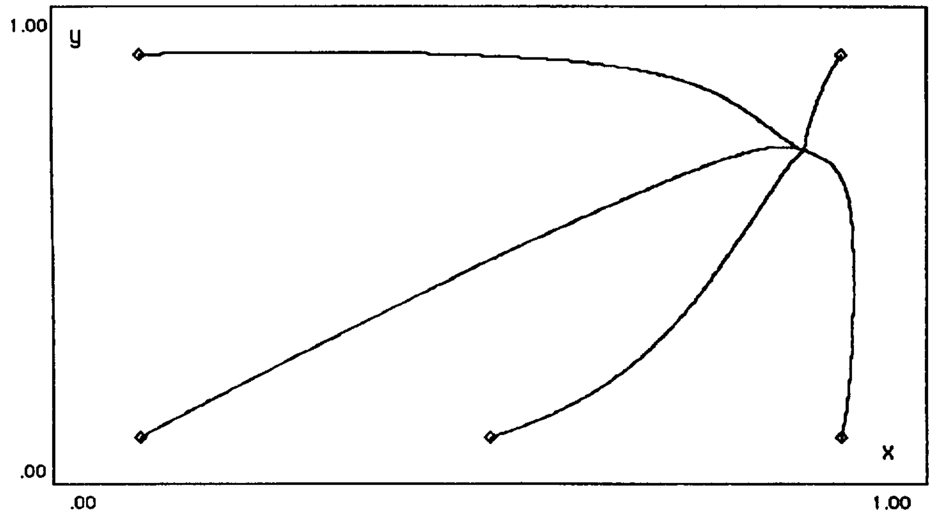

Figure 1. $G^1 = G^2 = G^{12} = G^{21} = 2$, $C^1 = C^2 = 4$, $C^{12} = 0.8$, $C^{21} = 1.4$. In this case, at equilibrium, individuals belonging to populations 1 and 2 are hawks and doves in proportions (x^*, y^*).

In summary, when $2G/C < 1$, there are three equilibrium points towards which the fast system may tend, (x^*, y^*), $((2G/C), 0)$, or $(0, (2G/C))$. Figure 1 shows a numerical simulation of the fast model using the Runge-Kutta method of the Case (a).

At the fast equilibrium, the subpopulation densities are as follows.

(a) $n_1^H = x^* n_1$, $n_1^D = (1 - x^*) n_1$, $n_2^H = y^* n_2$, $n_2^D = (1 - y^*) n_2$.
(b) $n_1^H = (2G/C) n_1$, $n_1^D = (1 - 2G/C) n_1$, $n_2^H = 0$, $n_2^D = 1$.
(c) $n_1^H = 0$, $n_1^D = 1$, $n_2^H = (2G/C) n_2$, $n_2^D = (1 - 2G/C) n_2$.
(d) According to the initial condition in $]0,1[\times]0,1[$, Cases (b) or (c).

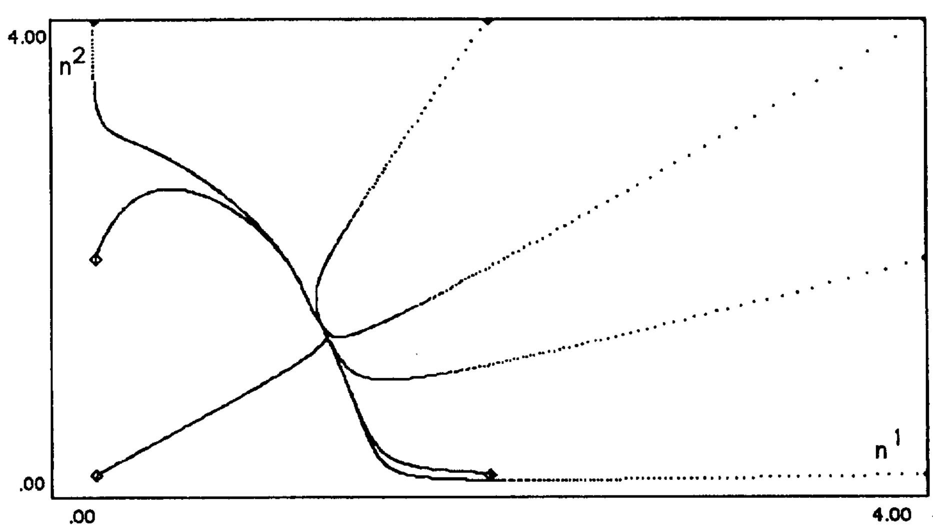

Figure 2. $G^1 = G^2 = G^{12} = G^{21} = 2$, $C^1 = C^2 = 4$, $C^{12} = 0.8$, $C^{21} = 1.4$. Coexistence of the two populations.

The aggregated model is given in equation (11). A calculation, given in Appendix B, shows that for the three different possible equilibrium points of the fast system, (x^*, y^*), $((2G/C), 0)$, or $(0, (2G/C))$, we have the following result:

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

This means that the point (u_1^*, u_2^*) is globally asymptotically stable. The two populations coexist in any case. Figure 2 shows a numerical simulation of the full model (7). We solved numerically the four equations and at each time the hawk and dove subpopulations are added to get the total densities of populations 1 and 2. As usual in competition models, the equilibrium densities of the aggregated model are smaller when the two populations are together, i.e., (u_1^*, u_2^*) than when alone, i.e., (1,1).

When the populations are together, the hawks fight not only with hawks of their own population but also with hawks of the other one. Thus, they get injuries from both sides and this has the effect of decreasing the equilibrium densities of the total populations.

4.2. The Case of Aggressive Individuals: All Hawks

In the case $2G/C > 1$, the point (1,1) can be a globally asymptotically fixed point. Figure 3 shows a numerical simulation of the fast model using the Runge-Kutta method where (1,1) is g.a.s.

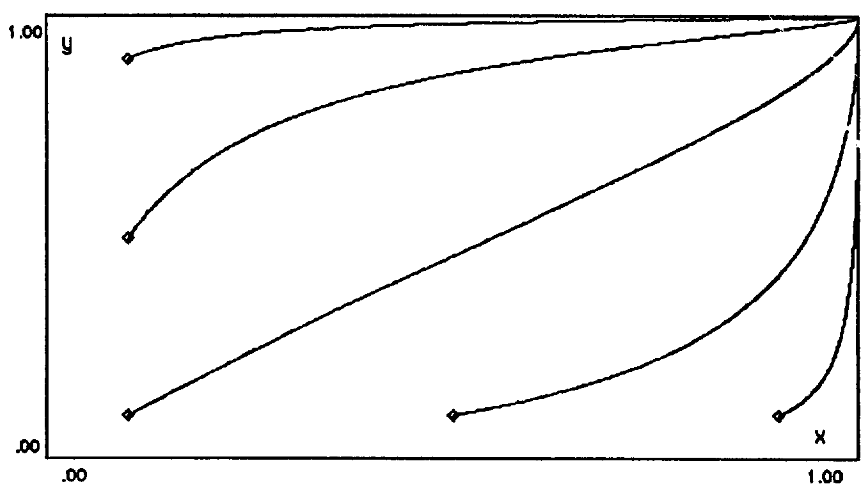

Figure 3. $G^1 = G^2 = G^{12} = G^{21} = 4$, $C^1 = C^2 = 2$, $C^{12} = 1$, $C^{21} = 3$. In this case, all individuals belonging to population 1 are doves at equilibrium while those of population 2 are hawks.

Assuming that the fast equilibrium is (1,1), i.e., that all individuals of both populations at the fast equilibrium are hawks, from equations (12), one can calculate the competition coefficients of the aggregated Lotka-Volterra model as follows:

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

Consequently, in this case of aggressive individuals, four cases occur.

(a) $C_{12} < C$ and $C_{21} < C$; then $0 < a_{12} < 1$, $0 < a_{21} < 1$, coexistence.
(b) $C_{12} > C$ and $C_{21} > C$; then $a_{12} > 1$, $a_{21} > 1$, exclusion. There is a separatrix.

According to initial conditions, either 1 or 2 wins.

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

Figure 4 shows a numerical simulation of the full model (7) in the Case (c).

The conclusion of this section is that when individuals are aggressive, they can coexist only when the costs of the conflicts between hawks of different populations are less than costs of those within the same population. In order to coexist, interpopulation injuries must be weaker than intrapopulation ones. This effect globally minimizes the costs and leads to coexistence.

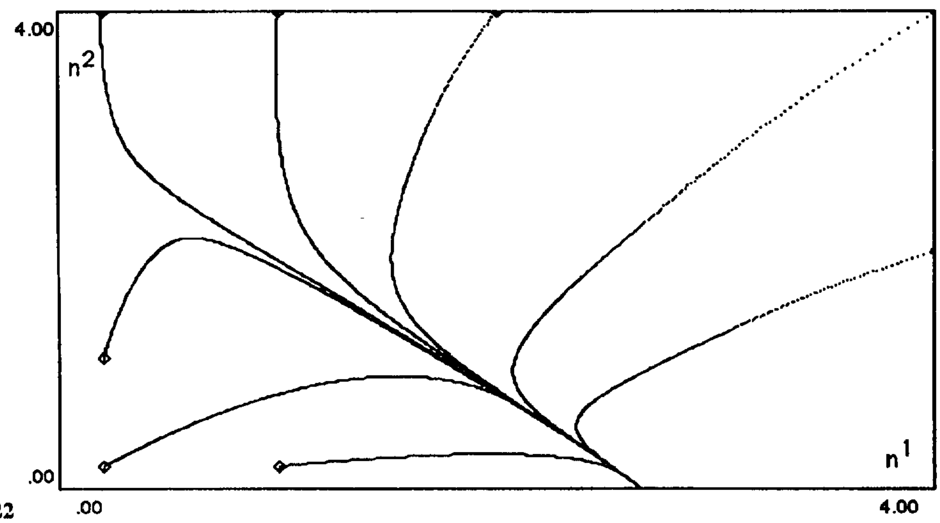

Figure 4. $G^1 = G^2 = G^{12} = G^{21} = 4$, $C^1 = C^2 = 2$, $C^{12} = 1$, $C^{21} = 3$. Mutual exclusion. Population 2 gets extinct.

5. CONCLUSION

The general conclusion of this article is that aggressive populations cannot coexist (except in the case of interpopulation costs being less than intra ones). Mixed populations of hawks and doves always coexist (in the case $2G < C$). To coexist, aggressiveness must be controlled.

In this article, we have limited our study to particular situations, i.e., when all the gains are equal and when the intrapopulation costs are equal for the two populations. We have also limited our study to particular fast equilibria, mainly mixed hawk and dove populations ($2G < C$) and all hawks. In the near future, we intend to continue this study and to obtain the solutions in all cases. The method that we have presented in this article can also be extended to more than two tactics only, to more than two populations, and to density-dependent game dynamics. This allows a large number of various situations involving many different cases of interest in population dynamics.

Another next step would be to establish connections with genetics model. This means that to hawk and doves tactics might be associated genotypes or phenotypes, [5–7]. In this way, one might replace the slow part of the system which describe the growth of the hawk and dove subpopulations by terms, taking into account the genetical rules of recombination (Hardy-Weinberg law) and also take into account the fights which, in a certain sense, play a role of selection due to the long term effects of the fights, injuries which can cause death due to fights between hawks, access to food sources, etc.

APPENDIX A
DERIVATION OF THE AGGREGATED MODEL

We start with model (7) that we recall

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

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

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

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

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. Let us add on the one hand the equations (7a) and (7b), and on the other hand (7c) and (7d) which 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 a particular fast equilibrium g.a.s. $(\bar{x}, \bar{y})$. To get the aggregated model, we must replace the hawk and dove subpopulations in terms of this fast equilibrium as follows:

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

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:

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

where $r = 2\gamma G$ and we have the following expressions (9) of the main text:

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

APPENDIX B
CALCULATION OF THE COMPETITION COEFFICIENTS OF THE AGGREGATED MODEL

We make the restriction of the study to the case $2G/C < 1$. As discussed in the main text, there are only three possibilities for the fast system, i.e., three equilibrium points g.a.s.:

$$(x^*, y^*) = \left(\frac{(2G - C_{12})}{C^2 - C_{12}C_{21}}, \frac{(2G - C_{21})}{C^2 - C_{12}C_{21}} \right), \quad \left(\frac{2G}{C}, 0 \right), \quad \text{and} \quad \left(0, \frac{2G}{C} \right).$$

The competition coefficients are given in equations (12) that we recall

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

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

B.1. Equilibrium Points $((2/C), 0)$ and $(0, (2G/C))$

When $C_{12} < C < C_{21}$, $((2G/C), 0)$ is g.a.s. When $C_{21} < C < C_{12}$, $(0, (2G/C))$ is g.a.s., and when $C_{12} > C$ and $C_{21} > C$, either $((2G/C), 0)$ or $(0, (2G/C))$ 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 $((2G/C), 0)$. To obtain the competition parameters of the aggregated model, let us substitute $((2G/C), 0)$ to $(\bar{x}, \bar{y})$ into equation (12). A simple calculation leads to the following expressions:

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

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

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

This equilibrium is smaller 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 $(0, (2G/C))$ is identical to the previous one for symmetry properties.

B.2. Equilibrium Point $(x^*, y^*) = ((2G - C_{12})/(C^2 - C_{12}C_{21}), (2G - C_{21})/(C^2 - C_{12}C_{21}))$

(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 first 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.

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