

## A predator–prey model with predators using hawk and dove tactics

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Received 22 December 2000; received in revised form 19 September 2001; accepted 12 October 2001

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### Abstract

In this work we present a predator–prey model that incorporates individual behavior of the predators. A classical Lotka–Volterra model with self-limiting prey describes the predator–prey interaction. Predator individuals can use two behavioral tactics to dispute a prey when they meet, the classical hawk and dove tactics. Each individual can use both tactics along its life. The predator behavioral change is described by means of a game dynamic model based upon the replicator equations, where the gain depends on prey density. We assume that the demographic process, predator–prey interactions, acts at a slow time scale in comparison with the evolution of the behavior of the predator population. The existence of two time scales allows studying the complete system from a reduced one, which describes the dynamics of the total predator and prey densities at the slow time scale. The aim of this work is to study the effects of individual predator behavior on the dynamics of the predator–prey system. The main conclusion that emerges from this study is the existence of a relationship between prey density and the strategy adopted by predators: aggressive behavior is connected to high prey and low predator densities, whereas a polymorphism dove–hawk is found at low prey and high predator densities. © 2002 Published by Elsevier Science Inc.

*Keywords:* Predator–prey model; Hawk–dove game; Aggregation methods; Coevolution

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## 1. Introduction

There are many observations showing that individuals may compete for resources, such as mate, territory or food [1]. When the resource items, for example prey for predators, have a heterogeneous distribution in the habitat, the probability of competition is thought to be enhanced. There are several reasons to expect that competitors vary in their ability to compete depending to the accessibility of the prey and/or the motivation of the other competitors. This competition, named interference, may arise through scramble or contest competition [2].

In a scramble competition, each predator exploits the resource as much as it can without aggression toward other competitors. Then the depletion of the resources affects all predators in the same way.

Alternatively, a predator can chase any other predator away from the prey and there are costs of chasing and fighting, which can be lower than the benefit of monopolizing the prey–resource. This situation is called a contest competition [2,3] and the outcome will depend on the strategies played by the opponents. Game theory is one way to explore this outcome and to find the optimal strategy, i.e. the evolutionary stable strategy (ESS) [4,5]. Scramble or contest competition may affect the dynamics of both predators and prey, which has rarely been investigated (see [6]).

In a real world, we would expect that each competitor will choose its strategy both in relation to the density of prey and in relation with the strategies adopted by the other competitors. An intuitive prediction is to observe aggressive behavior when the prey resource is difficult to find and/or when the density of prey is low. In this case, predators that are food-deprived, or when the density of prey is very low, should adopt an aggressive strategy in order to monopolize rare resources.

In this work we present a prey–predator model which incorporates individual behavior of the predators. Most classical prey–predator models do not take into account the behavioral structure of the population. Usually, the predator and the prey populations are assumed to be homogeneous, i.e. all individuals behave in a similar way. Here, having the problems previously presented, we shall take into account different tactics that predators can use for exploiting a common resource: the prey population.

As a first attempt to assemble in a model individual behavior and predator–prey relationship we make some simple assumptions. All individual predators hunt the same prey. We assume two stages in this process. At first, a predator catches a prey. In a second step, this predator has to fight with other predators to keep the prey. To simplify, we assume that once a prey is killed, a second predator is arriving and is disputing the prey to the predator that had caught the prey. This is an important simplification. In our model, fighting between predators only occur between two predators, the one that has caught a prey and a second one in the vicinity that is arriving to dispute the prey to the first predator. Under these conditions, predators fight together in order to keep or to have an access to a captured prey. We assume that individual predators can use two behavioral tactics to dispute a prey when they meet, the classical hawk and dove tactics.

The hawk is always aggressive and fights in any case. The dove is never aggressive and never escalates. When a hawk encounters a dove, it is always the winner and keeps the prey. When two hawks encounter, they fight. One of them is the winner and keeps the prey. However, both of them can receive injuries due to fighting. When two doves meet, they never fight and in average they share the prey. We assume that each individual predator can use both tactics along its life. In this

way, the same predator is not always hawk or dove but it can change tactics. At the occasion of an encounter, a predator could use the hawk tactic, but in some other occasion, it could use the dove tactic. After a certain number of encounters, we assume that, on the average, predators are using the tactic that gives them the better payoff. To describe the change of tactics of predators, we are going to use a game dynamic model based upon the replicator equations [7–9].

We also assume two different time scales:

- A fast time scale corresponds to the disputes and fights between the predators that occur each day.
- A slow time scale corresponds to the growth of the prey population, the mortality of the predator and the predator–prey interactions.

Assuming that predator–prey terms correspond to the slow time scale means that a few preys are killed each day in comparison to the total reservoir of preys. However, predators encounter and fight frequently (for example each day) to keep a captured prey or to dispute a prey to another predator. Consequently, the game dynamics correspond to the fast time scale.

We shall take advantage of the two time scales to reduce the dimension of the model and to obtain an aggregated model that describes the dynamics of the total predator and prey densities at the slow time scale [10–12].

The aim of this work is to study the effects of individual predator behavior on the dynamics of the predator–prey system. In particular, we shall look for the existence of different coexistence equilibria between the prey and the predator and the corresponding internal structures of the predator population: monomorphic, all hawk, or polymorphic, mixed hawk and dove. We are interested in the coevolution at the individual and community levels. We study the coupled dynamics of, on the one hand, predator changes of individual tactics at the fast time scale and, on the other hand, changes of the predator–prey community structure at the slow time scale.

In Section 2 we present, first of all, the game dynamic model, which represents the fast part of the complete system. Then the slow part of the system is built up based upon the classical Lotka–Volterra model with prey-density dependence. Finally, the model including the fast behavioral part and the slow demographic part is proposed. Section 3 is devoted to the construction and analysis of the so-called aggregated model. This model is a two-dimensional prey–predator model where, taking advantage of the two time scales, the game dynamics have disappeared and is taken into account in the parameters of the system. The interpretation of this study is developed in Section 4. Section 5 is devoted to draw general conclusions. Finally some details of the mathematical analysis of the model are given in Appendix A.

## 2. The predator–prey model

Let  $n(t)$  be the size of the prey population and  $p(t)$  the total size of the predator population at time  $t$ . The model is composed of two parts, a fast part that describes the change of tactics of predators and a slow part that describes the growth of the prey population, the predator mortality and the predator–prey interactions.

2.1. *Predators game dynamics at the fast time scale*

Assume that predators are divided into two sub-groups, hawk and dove. Let  $p_H(t)$  and  $p_D(t)$  be respectively the hawk and dove predator densities at time  $t$ . The total density of predators is given by

$$p(t) = p_H(t) + p_D(t). \tag{1}$$

Predators fight to keep or to get access to a captured prey. This process occurs at the fast time scale. At the occasion of each encounter, each predator must adopt either the hawk or the dove tactic. The classical hawk–dove game describes this process of conflicts between two predators. In our case, the gain  $G$  of the game corresponds to the prey amount that two predators dispute each day. This amount of preys killed per unit time (for example each day) and per predator is the classical functional response. To simplify, we assume a classical type I functional response, that is a linear functional response which is also the gain  $G(n)$  of the game

$$G(n) = an, \tag{2}$$

where  $a$  is a positive parameter. In the hawk case, the predator is always aggressive. When two hawks fight, they can get wounded. Let  $C$  be the cost due to fightings between hawks.  $C$  is a positive parameter.

Let us recall that a coefficient  $a_{ij}$  of the payoff matrix corresponds to the gain that is obtained by an individual playing tactic  $i$  against an individual playing tactic  $j$ . When two hawks meet, they share the gain on the average but also the cost due to injuries,  $a_{HH} = (G - C)/2$ . When a hawk meets a dove, it always obtains the gain,  $a_{HD} = G$ , while the dove retreats and gets nothing,  $a_{DH} = 0$ . When two doves meet, they share the gain but also they have no cost,  $a_{DD} = G/2$ . Consequently, the payoff matrix  $\mathbf{A}$  is the classical hawk–dove one

$$\mathbf{A} = \begin{matrix} & \begin{matrix} \text{H} & \text{D} \end{matrix} \\ \begin{pmatrix} \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix} & \begin{matrix} \text{H} \\ \text{D} \end{matrix} \end{matrix}. \tag{3}$$

Let  $x(t)$  and  $y(t)$  be respectively the hawks and doves proportions in the population of predators at time  $t$

$$x(t) = \frac{p_H(t)}{p(t)}, \quad y(t) = 1 - x(t) = \frac{p_D(t)}{p(t)}. \tag{4}$$

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

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

The gain  $\Delta_D$  of an individual always playing the dove strategy is the following one:

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

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

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

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

$$\begin{cases} \frac{dx}{d\tau} = x(\Delta_H - \Delta), \\ \frac{dy}{d\tau} = y(\Delta_D - \Delta). \end{cases} \tag{5}$$

Using this model, we assume that if a tactic brings a better payoff than the average payoff of the population, the proportion of individuals playing this strategy is increasing and conversely. In the previous equations,  $\tau$  is the fast time scale. Thus, we assume that the hawk–dove game is fast in comparison to other processes that we shall now consider in the model, such as predator mortality, prey growth and captures of preys by predators.

### 2.2. Dynamics of prey density at the slow time scale

Preys killed by predators constitute a common resource for predators. We assume a very simple equation for the total prey density, a classical Lotka–Volterra model with self-limiting prey [13]

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) - anp, \tag{6}$$

where  $t$  corresponds to the slow time scale. As usual, we have the following relationship between the two time scales,  $t = \varepsilon\tau$ . According to the previous equation, in absence of predators, the prey population grows depending on a logistic equation with an intrinsic growth rate  $r$  towards a carrying capacity  $K$ . Furthermore, we assume a Lotka–Volterra functional response of type I.  $a$  is a positive parameter, the predation force parameter and is the same as the one used in the functional response which is also the gain  $G(n)$  of the game.

### 2.3. Dynamics of predator densities at the slow time scale

For predators, we assume a constant natural mortality rate  $\mu$  identical for hawks and doves,  $\mu > 0$ . For the predator equations, we assume that the growth rate of each sub-group, hawk (resp. dove), is proportional to the average payoff obtained by an individual using the hawk (resp. dove) tactic on the occasion of each type of encounter, hawk–hawk or hawk–dove for a hawk (resp. dove–hawk or dove–dove for a dove). These average payoffs must be weighted by the proportion of each type of encounters. For example, a hawk can encounter either another hawk in proportion  $p_H/p$  and gets the gain  $(G - C)/2$  or a dove in proportion  $p_D/p$  and gets  $G$ . As a consequence, the growth of the predator hawk sub-population obeys the following equation:

$$\frac{dp_H}{dt} = -\mu p_H + \left( \alpha \left( \frac{G-C}{2} \right) \frac{p_H}{p} + \alpha G \frac{p_D}{p} \right) p_H, \quad (7)$$

where  $\alpha$  is a conversion positive coefficient of gain and cost into biomass of predators. With similar assumptions for the dove sub-population of predators, we obtain

$$\frac{dp_D}{dt} = -\mu p_D + \alpha \frac{G}{2} \frac{p_D}{p} p_D. \quad (8)$$

The predator growth is assumed to be slow in comparison to the game dynamics. This can be interpreted in the sense that few preys are captured each day but predators fight frequently to keep them or dispute them to other predators.

#### 2.4. The complete slow–fast predator–prey model

The complete model combines both fast and slow processes in a similar way than in our previous articles [14–17]. The complete model reads

$$\begin{cases} \varepsilon \frac{dn}{dt} = \varepsilon \left( rn \left( 1 - \frac{n}{K} \right) - anp \right), \\ \varepsilon \frac{dp_H}{dt} = px(\Delta_H - \Delta) + \varepsilon \left( -\mu p_H + \left( \alpha \left( \frac{G-C}{2} \right) \frac{p_H}{p} + \alpha G \frac{p_D}{p} \right) p_H \right), \\ \varepsilon \frac{dp_D}{dt} = py(\Delta_D - \Delta) + \varepsilon \left( -\mu p_D + \alpha \frac{G}{2} \frac{p_D}{p} p_D \right), \end{cases} \quad (9)$$

where  $\varepsilon \ll 1$  is a small parameter. It is also usual to use the fast time scale  $\tau$

$$\begin{cases} \frac{dn}{d\tau} = \varepsilon \left( rn \left( 1 - \frac{n}{K} \right) - anp \right), \\ \frac{dp_H}{d\tau} = px(\Delta_H - \Delta) + \varepsilon \left( -\mu p_H + \left( \alpha \left( \frac{G-C}{2} \right) \frac{p_H}{p} + \alpha G \frac{p_D}{p} \right) p_H \right), \\ \frac{dp_D}{d\tau} = py(\Delta_D - \Delta) + \varepsilon \left( -\mu p_D + \alpha \frac{G}{2} \frac{p_D}{p} p_D \right). \end{cases} \quad (10)$$

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

### 3. The aggregated predator–prey model

We shall now take advantage of the two time scales to reduce the dimension of the complete system (9) of three equations into a system of two equations. For aggregation methods, we refer to [10,11,18,19]. In the next step, we shall proceed to the analysis of this ‘aggregated’ model which will be simpler to study than the complete one.

### 3.1. Derivation of the aggregated model

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

$$\begin{cases} \frac{dp_H}{d\tau} = px(\Delta_H - \Delta), \\ \frac{dp_D}{d\tau} = py(\Delta_D - \Delta). \end{cases} \tag{11}$$

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

$$\frac{dx}{dt} = \frac{x}{2}(1 - x)(G - Cx). \tag{12}$$

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

- $G < C$ ,  $x^* = G/C$  is asymptotically stable for any initial condition  $0 < x(0) < 1$ . In this case, at equilibrium, the population is polymorphic with a proportion  $G/C$  of hawks and  $1 - G/C$  of doves.
- $G > C$ ,  $G/C$  does not belong to the interval  $[0, 1]$ . The equilibrium  $x^* = 1$  is asymptotically stable. The population is monomorphic and totally hawk at equilibrium.

In order to aggregate, we make the assumption that the fast process is at the fast equilibrium. Thus, we come back to the complete initial system (9), substitute the previous fast equilibrium and add the two predator equations. It is necessary to replace the fast variables in terms of the fast equilibrium as follows:

$$p_H = x^*p, \quad p_D = (1 - x^*)p.$$

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

$$\begin{cases} \frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) - anp + o(\varepsilon), \\ \frac{dp}{dt} = -\mu p + \frac{\alpha G}{2}p - \frac{\alpha C}{2}(x^*)^2p + o(\varepsilon). \end{cases} \tag{13}$$

In the previous equations, we used a term  $o(\varepsilon)$ . This means that the aggregated model is given by the two previous equations to which further terms should be added. It can be shown that the complete aggregated model is a Taylor expansion in terms of the powers of the small parameter  $\varepsilon$ . These further terms of the series could be calculated if necessary. If we neglect these terms of the order of  $\varepsilon$ , the aggregated model simply reads

$$\begin{cases} \frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) - anp, \\ \frac{dp}{dt} = -\mu p + \frac{\alpha G}{2}p - \frac{\alpha C}{2}(x^*)^2p. \end{cases} \tag{14}$$

The dynamics of system (14) are a good approximation of the real dynamics if two conditions are met:

- The system is structurally stable, which is the case.
- $\varepsilon$  is small enough, which is assumed.

In our case, we remember that we can have two possibilities for the fast equilibrium and that the gain depends on the prey density as follows, see Eq. (2):

$$G(n) = an.$$

As a consequence, according to the prey density, we obtain two different aggregated models which are valid on two domains of the phase plane:

*Model I:*  $n < \frac{C}{a}$ ,  $x^* = \frac{an}{C}$  is asymptotically stable in Eq. (12),

$$\begin{cases} \frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right) - anp, \\ \frac{dp}{dt} = -\mu p + \frac{\alpha a}{2} np - \frac{\alpha a^2}{2C} n^2 p. \end{cases} \quad (15)$$

*Model II:*  $n > \frac{C}{a}$ ,  $x^* = 1$  is asymptotically stable in Eq. (12),

$$\begin{cases} \frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right) - anp, \\ \frac{dp}{dt} = -\mu p + \frac{\alpha a}{2} np - \frac{\alpha C}{2} p. \end{cases} \quad (16)$$

These two models connect at the vertical line  $n = C/a$  of the phase space  $(n, p)$ .

### 3.2. Study of the dynamics of the aggregated model

The  $dn/dt = 0$  nullclines are the same for both models I and II. The nullclines are two straight lines: the line  $n = 0$  and the line with a negative slope whose equation is

$$p = \frac{r}{a} \left(1 - \frac{n}{K}\right). \quad (17)$$

Now, let us look for the  $dp/dt = 0$  nullclines. We have several different cases depending on parameters values. For model I, system (15), if  $\alpha C < 8\mu$ , the only  $dp/dt = 0$  nullcline is  $p = 0$ , and if  $\alpha C > 8\mu$ , we have besides  $p = 0$  two more  $dp/dt = 0$  nullclines which are vertical lines

$$n = n_1^* = \frac{C}{2a} - \frac{\sqrt{\alpha a^2 C (\alpha C - 8\mu)}}{2\alpha a^2}$$

and

$$n = n_2^* = \frac{C}{2a} + \frac{\sqrt{\alpha a^2 C (\alpha C - 8\mu)}}{2\alpha a^2}.$$

For model II, system (16), we have two  $dp/dt = 0$  nullclines,  $p = 0$  and the vertical line

$$n = n_3^* = \frac{2\mu + \alpha C}{\alpha a}.$$



The vertical nullclines are ordered in the following way:

$$0 < n_1^* < \frac{C}{2a} < n_2^* < \frac{C}{a} < n_3^*, \tag{18}$$

so  $n = n_1^*$  and  $n = n_2^*$  are always, if they exist, in the domain of model I, system (15), while  $n = n_3^*$  is always found in the domain of model II, system (16).

Now, let us look for the equilibria.  $(0, 0)$  and  $(0, K)$  are two equilibria that always exist. Three other equilibria  $(n_1^*, p_1^*)$ ,  $(n_2^*, p_2^*)$  and  $(n_3^*, p_3^*)$ , where

$$p_i^* = \frac{r}{a} \left( 1 - \frac{n_i^*}{K} \right), \quad i \in \{1, 2, 3\} \tag{19}$$

can be found in the positive quadrant provided that  $p_i^* > 0$ , that is  $n_i^* < K$ .

We can notice that due to the fact that the two axes,  $n = 0$  and  $p = 0$ , are invariant, the positive quadrant is also invariant.

For any parameters values, it can be shown that the origin is a saddle, see Appendix A.

According to parameters values, the phase portraits could be grouped into six categories that are shown on Figs. 1 and 2.

Fig. 1 corresponds to the case  $\alpha C < 8\mu$ . When  $K > n_3^* > C/a$ , 1 (a), the equilibrium  $(K, 0)$  is a saddle and the positive equilibrium  $(n_3^*, p_3^*)$  is globally asymptotically stable, so the prey and the predator coexist, whereas for  $n_3^* > K > C/a$ , 1 (b), the equilibrium  $(K, 0)$  is globally asymptotically stable, which means that the predator gets extinct and the prey tends to its carrying capacity.

Fig. 2 corresponds to the case  $\alpha C > 8\mu$  and it is subdivided into four cases according to the position of  $K$  with respect to the other three prey equilibrium values:  $n_1^*$ ,  $n_2^*$  and  $n_3^*$ .

Fig. 2(a) corresponds to the subcase  $n_3^* < K$ . The equilibrium  $(K, 0)$  is a saddle. There are three positive equilibria:  $(n_1^*, p_1^*)$ , which is a stable focus,  $(n_2^*, p_2^*)$ , which is a saddle, and  $(n_3^*, p_3^*)$ , which is a stable focus. There exists a separatrix. According to initial conditions, either the trajectory tends to  $(n_1^*, p_1^*)$  or to  $(n_3^*, p_3^*)$ . In that case, preys and predators always coexist, though at different density levels. For the prey density it is verified  $n_3^* > n_1^*$  while for the predator density the converse inequality,  $p_3^* < p_1^*$ , holds.

Fig. 2(b) describes the subcase  $n_2^* < K < n_3^*$ . The equilibrium  $(K, 0)$  is a stable node. There are two positive equilibria:  $(n_1^*, p_1^*)$ , which is a stable focus, and  $(n_2^*, p_2^*)$ , which is a saddle point. There

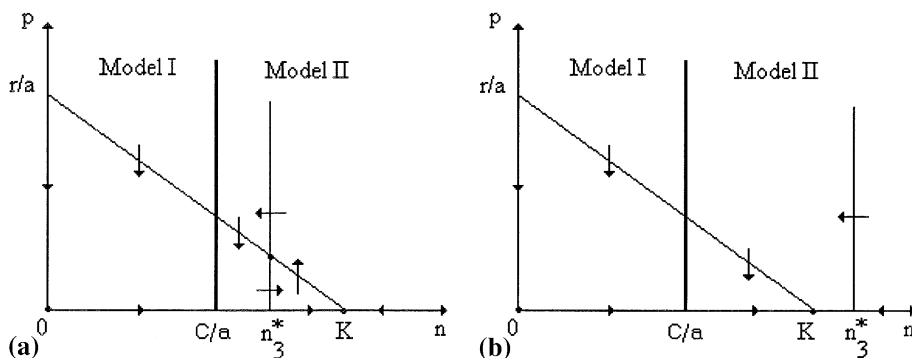


Fig. 1. Phase portrait of the aggregated system when  $\alpha C < 8\mu$ : (a)  $K > n_3^*$  and (b)  $K < n_3^*$ .

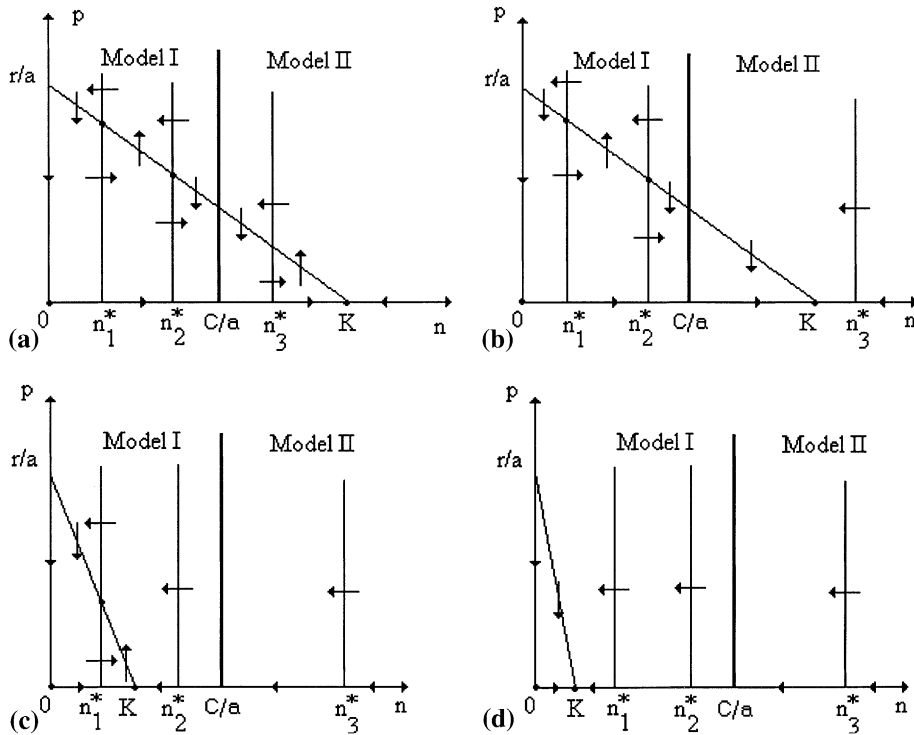


Fig. 2. Phase portrait of the aggregated system when  $\alpha C > 8\mu$ : (a)  $n_3^* < K$ , (b)  $n_2^* < K < n_3^*$ , (c)  $n_1^* < K < n_2^*$  and (d)  $K < n_1^*$ .

is also a separatrix marking the boundary of the basins of attraction of the two stable equilibria. Depending on initial conditions, either the trajectory tends to  $(K, 0)$  or to  $(n_1^*, p_1^*)$ . So, either the predator goes to extinction or the prey and the predator coexist.

The subcase  $n_1^* < K < n_2^*$  is shown in Fig. 2(c). The equilibrium  $(K, 0)$  is a saddle point. There is only one positive equilibrium  $(n_1^*, p_1^*)$  which is a stable focus. So preys and predators coexist.

Finally, Fig. 2(d) illustrates the case  $K < n_1^*$ . The equilibrium  $(K, 0)$  is a stable node. The predator always gets extinct and the prey tends to its carrying capacity.

#### 4. Discussion

From a mathematical point of view, we have distinguished six different phase portraits. From an ecological point of view, we could take into account four possibilities concerning the stability in the prey–predator relationship: coexistence, predator exclusion, coexistence or predator exclusion depending on initial conditions, and coexistence at two different density levels depending on initial conditions. Moreover we could pay attention to the behavioral composition of the predator population at equilibrium.

In the cases of Figs. 1(a) and 2(c), predator and prey coexist. Fig. 3 shows a typical phase portrait of these coexistence cases. It shows the results of a Runge–Kutta simulation with  $r = 10$ ,

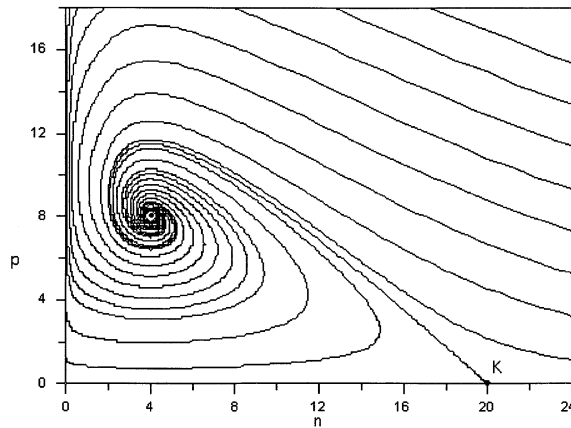


Fig. 3. Coexistence. Phase portrait of the aggregated system for parameters values:  $r = 10$ ,  $K = 20$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 2$  and  $\mu = 1$ .

$K = 20$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 2$ ,  $\mu = 1$ . However, there are differences between these two cases. On Fig. 1(a), the stable equilibrium belongs to model II and this signifies that the predator population is monomorphic hawk. On Fig. 2(c), the stable equilibrium belongs to model I and consequently the predator population is polymorphic with the corresponding proportions of hawk and dove individuals.

In cases of Figs. 1(b) and 2(d), the predator goes to extinction and the prey tends to its carrying capacity. Fig. 4 shows the typical phase portrait of the aggregated model for  $r = 10$ ,  $K = 2$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 10$ ,  $\mu = 1$ . On Fig. 1(b), the equilibrium  $(K, 0)$  belongs to model II and thus the predator is monomorphic hawk when approaching extinction. On Fig. 2(d), the equilibrium  $(K, 0)$  belongs to model I and thus the predator is polymorphic when getting extinct. Consequently, although in both cases, there is predator extinction, this process occurs for two different behavioral compositions of the predators population.

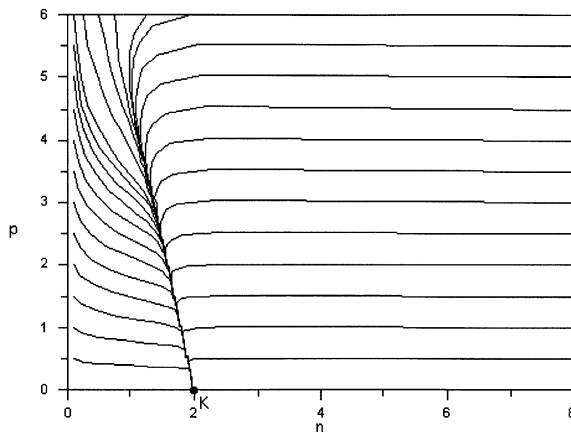


Fig. 4. Predator exclusion. Phase portrait of the aggregated system for parameters values:  $r = 10$ ,  $K = 2$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 10$  and  $\mu = 1$ .

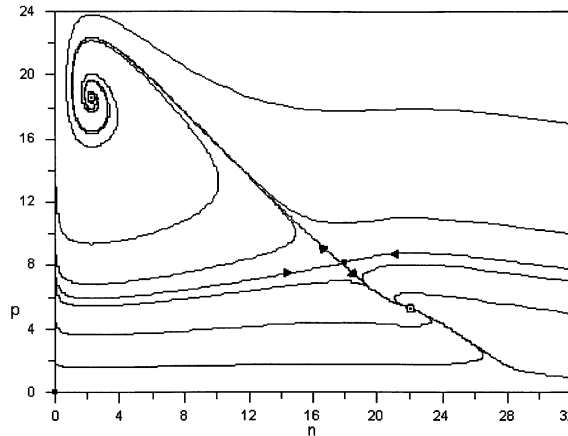


Fig. 5. Coexistence at two different density and behavioral levels. Phase portrait of the aggregated system for parameters values:  $r = 20$ ,  $K = 30$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 20$  and  $\mu = 1$ .

In case of Fig. 2(a), there is a separatrix. There are two stable equilibria. According to the initial condition, the prey and the predator coexist at one of these equilibria. Fig. 5 shows the phase portrait of the aggregated system with  $r = 20$ ,  $K = 30$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 20$ ,  $\mu = 1$ . We have two stable equilibria,  $(n_1^*, p_1^*)$  belonging to model I (predators are polymorphic) and  $(n_3^*, p_3^*)$  belonging to model II (predator are monomorphic). We observe here for predators a connection between the degree of aggressiveness and the density level: low aggressiveness degree at high density level, and high aggressiveness degree at low density level. This kind of result was already found in the case of the study of a domestic cat population [15,17]; in rural areas, low density, most of the individuals are aggressive while in urban areas, high density, most of them are dove.

In case of Fig. 2(b), there is again a separatrix. According to the initial conditions, the predator and the prey coexist (at low density) or the predator goes to extinction and the prey tends to its carrying capacity. Fig. 6 shows the phase portrait of the aggregated model with  $r = 10$ ,  $K = 11$ ,

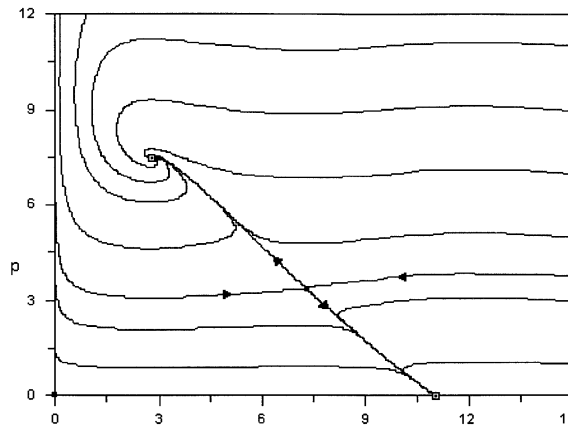


Fig. 6. Coexistence and exclusion. Phase portrait of the aggregated system for parameters values:  $r = 10$ ,  $K = 11$ ,  $a = 1$ ,  $\alpha = 1$ ,  $C = 10$  and  $\mu = 1$ .

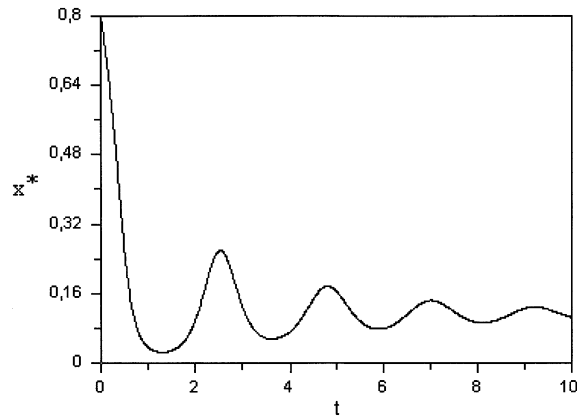


Fig. 7. The proportion of hawks versus time when the solution of the aggregated model is spiraling towards the polymorphic stable equilibrium  $(n_1^*, p_1^*)$ .

$a = 1$ ,  $\alpha = 1$ ,  $C = 10$ ,  $\mu = 1$ . Both stable equilibria belong to different models,  $(n_1^*, p_1^*)$  to model I, where predators are monomorphic hawk, and  $(K, 0)$  to model II, where predators are polymorphic. We notice that the predator extinction occurs when all predators are hawk while there is coexistence when predators are mixed hawk and dove. Polymorphism is related to coexistence.

Fig. 7 shows the time evolution of the proportion of hawks when the trajectory of the aggregated model is slowly spiraling to the polymorphic stable equilibrium  $(n_1^*, p_1^*)$  of model II. The fast equilibrium defines the behavioral structure of the predator population but the fact that it depends on prey density entails its evolution at the slow time scale along the trajectory of the aggregated model.

## 5. Conclusion

Few theoretical studies aimed to link behaviour and population dynamics. The use of dynamic modelling was one tentative approach to investigate this [20]. Our mathematical approach is a promising alternative that combines ESS and population demography.

The main conclusion that emerges from this study is the existence of a relationship between prey density (i.e. carrying capacity) and the strategy adopted by predators. Aggressive behaviour (hawk strategy) is an ESS in high prey densities, whereas a polymorphism with the presence of both doves and hawks, is found in low prey densities. This result is rather counter-intuitive as, based on verbal arguments, we have expected an increase of contest competition in low prey accessibility (i.e. low density).

An alternative view is that aggressive behaviour is not advantageous when prey are rare and collaboration should be favored [21]. Hence, in high prey densities the invasion of aggressive predators is facilitated and there is no need for collaboration. Moreover, there is a strong connection between the strategies adopted and density of predators. The equilibrium populations of predators are always higher when polymorphism in strategies occurs, which seems to be more intuitive as we have expected that the energy devoted to contest is at the expense of growth and

reproduction. This reinforces the above conclusion, aggressive predators can only invade when prey densities are high. We could also view it in relation with group size. Hence, in low prey densities, group size of predators should be high and composed mainly with co-operative individuals (dove strategies), whereas in high prey densities individuals and aggressive predators (hawk strategy) should be favoured.

### Acknowledgements

This work is partially supported by Proyecto de Investigación PB98-0702 (Spanish M.E.C.).

### Appendix A. Local stability of the equilibria

#### A.1. Case of model I

The Jacobian matrix for model I, system (15), is the following one:

$$J = \begin{pmatrix} r \left(1 - \frac{2n}{K}\right) - ap & -an \\ \frac{\alpha a}{2}p - \frac{\alpha a^2}{C}np & -\mu + \frac{\alpha a}{2}n - \frac{\alpha a^2}{2C}n^2 \end{pmatrix}.$$

At the origin, we have

$$J = \begin{pmatrix} r & 0 \\ 0 & -\mu \end{pmatrix},$$

with two real eigenvalues with opposite signs. The origin is a saddle point.

When the equilibrium  $(K, 0)$  is in the domain of model I, i.e.  $K < C/2a$ , the Jacobian matrix reads

$$J = \begin{pmatrix} -r & -aK \\ 0 & -\mu + \frac{\alpha a}{2}K - \frac{\alpha a^2}{2C}K^2 \end{pmatrix}.$$

One eigenvalue is negative,  $\lambda_1 = -r$  and the second one is  $\lambda_2 = -\mu + (\alpha a/2)K - (\alpha a^2/2C)K^2$ . As  $n_1^*$  and  $n_2^*$  are the roots of the polynomial  $-\mu + (\alpha a/2)x - (\alpha a^2/2C)x^2$ , if they do not exist ( $\alpha c < 8\mu$ ), then  $\lambda_2$  is also negative and so  $(K, 0)$  is stable. When  $n_1^*$  and  $n_2^*$  exist ( $\alpha c > 8\mu$ ) then the condition for  $\lambda_2 < 0$  to hold is  $K \in (0, n_1^*) \cup (n_2^*, \frac{C}{a})$ .

For both equilibria  $(n_1^*, p_1^*)$  and  $(n_2^*, p_2^*)$ , after some algebra, the Jacobian matrix reduces to

$$J = \begin{pmatrix} -r \frac{n_i^*}{K} & -an_i^* \\ \frac{\alpha a^2}{C} \left(\frac{C}{2a} - n_i^*\right) p_i^* & 0 \end{pmatrix},$$

where it is obvious that when the point belongs to the positive quadrant, the trace of the Jacobian matrix is negative and, consequently, if the determinant is positive then the equilibrium is stable, while otherwise it is a saddle point. The determinant is the next expression:

$$\frac{\alpha a^3}{C} \left( \frac{C}{2a} - n_i^* \right) n_i^* p_i^*.$$

Thus, having in mind expression (18), we have  $n_1^* < C/2a < n_2^*$ , and so when  $(n_1^*, p_1^*)$  belongs to the positive quadrant, it is always stable while when  $(n_2^*, p_2^*)$  belongs to the positive quadrant, it is always a saddle point.

Summarizing the results of model I:

- If  $\alpha c < 8\mu$ , equilibria:  $(K, 0)$  stable.
- If  $\alpha c > 8\mu$  and  $K < n_1^* < n_2^*$ , equilibria:  $(K, 0)$  stable (Fig. 2(d)).
- If  $\alpha c > 8\mu$  and  $n_1^* < K < n_2^*$ , equilibria:  $(n_1^*, p_1^*)$  stable and  $(K, 0)$  unstable (Fig. 2(c)).
- If  $\alpha c > 8\mu$  and  $n_1^* < n_2^* < K$ , equilibria:  $(n_1^*, p_1^*)$  stable,  $(n_2^*, p_2^*)$  unstable and  $(K, 0)$  stable.

### A.2. Case of model II

The Jacobian matrix for model II, system (16), is the following one:

$$J = \begin{pmatrix} r \left( 1 - \frac{2n}{K} \right) - ap & -an \\ \frac{\alpha a}{2} p & -\mu + \frac{\alpha a}{2} n - \frac{\alpha C}{2} \end{pmatrix}.$$

In the case of the equilibrium  $(K, 0)$ , the Jacobian matrix simplifies to

$$J = \begin{pmatrix} -r & -aK \\ 0 & -\mu + \frac{\alpha a}{2} K - \frac{\alpha C}{2} \end{pmatrix},$$

where one of the eigenvalues is always negative,  $\lambda_1 = -r$ , while the second one,  $\lambda_2 = -\mu + (\alpha a/2)K - (\alpha C/2)$ , is negative if  $K < n_3^*$  and positive if  $K > n_3^*$ . Consequently, the equilibrium  $(K, 0)$  is a stable node if  $K < n_3^*$  and a saddle point if  $K > n_3^*$ .

For the equilibrium  $(n_3^*, p_3^*)$ , after some algebra, the Jacobian matrix reduces to

$$J = \begin{pmatrix} -r \frac{n_3^*}{K} & -an_3^* \\ \frac{\alpha a}{2} p_3^* & 0 \end{pmatrix}.$$

so it is straightforward that when it belongs to the positive quadrant, the trace of the Jacobian matrix is negative and the determinant is positive which implies stability.

Summarizing the results of model II:

- If  $K < n_3^*$ , equilibria:  $(K, 0)$  stable (Figs. 1(b) and 2(b)).
- If  $K > n_3^*$ , equilibria:  $(n_3^*, p_3^*)$  stable and  $(K, 0)$  unstable (Figs. 1(a) and 2(a)).

### References

[1] A. Manning, M.S. Sawkins, An introduction to Animal Behaviour, Cambridge University, Cambridge, 1998.  
 [2] M. Milinski, G.A. Parker, Competition for resources, in: J.R. Krebs, N.B. Davies (Eds.), Behavioural Ecology, Blackwell, Oxford, 1991, p. 137.

- [3] S.E. Riechert, Game theory and animal contests, in: L.A. Dugatkin, H.K. Reeve (Eds.), *Game Theory and Animal Behavior*, Oxford University, Oxford, 1998, p. 64.
- [4] J. Maynard Smith, G. Price, The logic of animal conflict, *Nature* 246 (1973) 15.
- [5] J. Maynard Smith, *Evolution and The Theory of Games*, Cambridge University, Cambridge, 1982.
- [6] A. Lomnicki, *Population Ecology of Individuals*, Princeton University, Princeton, NJ, 1988.
- [7] J. Hofbauer, K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University, Cambridge, 1998.
- [8] R. Cressman, *The Stability Concept of Evolutionary Game Theory*, Springer, Berlin, 1992.
- [9] M. Mesterton-Gibbons, *An Introduction to Game-Theoretic Modell.*, Addison-Wesley, Redwood City, 1992.
- [10] P. Auger, R. Bravo de la Parra, Methods of aggregation of variables in population dynamics, *C.R. Acad. Sci. Paris, Life Sci.* 323 (2000) 665.
- [11] R. Bravo de la Parra, P. Auger, E. Sánchez, Aggregation methods in discrete models, *J. Biol. Syst.* 3 (1995) 603.
- [12] C. Bernstein, P. Auger, J.-C. Poggiale, Predator migration decisions, the ideal free distribution and predator–prey dynamics, *Am. Nat.* 153 (1999) 267.
- [13] W.S.C. Gurney, R.M. Nisbet, *Ecological Dynamics*, Oxford University, Oxford, 1998.
- [14] E. Sánchez, P. Auger, R. Bravo de la Parra, Influence of individual aggressiveness on the dynamics of competitive populations, *Acta Biotheoret.* 45 (1997) 321.
- [15] P. Auger, D. Pontier, Fast game theory coupled to slow population dynamics: the case of domestic cat populations, *Math. Biosci.* 148 (1998) 65.
- [16] P. Auger, R. Bravo de la Parra, E. Sánchez, Hawk–dove games and competition dynamics, *Math. Comput. Modell.* 27 (1998) 89.
- [17] D. Pontier, P. Auger, R. Bravo de la Parra, E. Sánchez, The impact of behavioral plasticity at individual level on domestic cat population dynamics, *Ecol. Modell.* 133 (2000) 117.
- [18] Y. Iwasa, V. Andreassen, S.A. Levin, Aggregation in model ecosystems I. Perfect aggregation, *Ecol. Modell.* 37 (1987) 287.
- [19] Y. Iwasa, S.A. Levin, V. Andreassen, Aggregation in model ecosystems II. Approximate aggregation, *IMA J. Math. Appl. Med. Biol.* 6 (1989) 1.
- [20] M. Mangel, C.W. Clark, *Dynamic Modelling in Behavioral Ecology*, Princeton University, Princeton, NJ, 1988.
- [21] D.M. Kitchen, C. Packer, Complexity in vertebrate societies, in: L. Keller (Ed.), *Levels of Selection in Evolution*, Princeton University, Princeton, NJ, 1999, p. 176.