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Bifurcation analysis of a predator–prey model with predators using hawk and dove tactics

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Abstract

Most classical prey–predator models do not take into account the behavioural structure of the population. Usually, the predator and the prey populations are assumed to be homogeneous, i.e. all individuals behave in the same way. In this work, we shall take into account different tactics that predators can use for exploiting a common self-reproducing resource, the prey population. Predators fight together in order to keep or to have access to captured prey individuals. Individual predators can use two behavioural tactics when they encounter to dispute a prey, the classical hawk and dove tactics. We assume two different time scales. The fast time scale corresponds to the inter-specific searching and handling for the prey by the predators and the intra-specific fighting between the predators. The slow time scale corresponds to the (logistic) growth of the prey population and mortality of the predator. We 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. We present the bifurcation analysis of the model and the effects of the different predator tactics on persistence and stability of the prey–predator community are discussed.

Keywords: Hawk–dove tactics; Predator–prey model; Slow–fast dynamics; Aggregation of variables; Bifurcation analysis

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1. Introduction

An important issue in population dynamics is to understand the effects of individual tactics that may adopt individuals at the population and community levels. Individuals compete for mating, food and territory. Different behavioural traits (Lott, 1991; Stamps and Buechner, 1985) occur among individuals of the same population and between different populations (Stamps and Buechner, 1985; Perret and Blondel, 1993; Pontier et al., 1995). Some phenotypic characteristics, such as aggressivity, can differ between populations. For example, in urban populations, domestic cats rarely fight while in rural populations, individuals are more likely to be aggressive for mating and to get access to some resource, (Liberg and Sandell, 1988; Pontier et al., 1995; Auger and Pontier, 1998; Pontier et al., 2000). Individuals are capable of learning and to change tactics along their life time according to the environmental conditions, to their age, to their physical conditions and to the results of previous contests (Wolf and Waltz, 1993; Liberg, 1981; Yamane et al., 1996). Behavioural plasticity allows an individual to be more flexible and to adopt the behaviour that can maximize its survival in the present environmental condition.

In previous works (Auger and Pontier, 1998; Pontier et al., 2000), we investigated the effects of aggressiveness

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on population dynamics. In these articles, individuals competed for some resource and the model was aimed at looking for the effects of this competition on the level of equilibrium density of the total population in the long term. The competition process was described by the classical hawk–dove model occurring at the fast time scale which was coupled to a population dynamics model at a slow time scale. This model was able to show the relationship between the equilibrium density of the population which was a decreasing function of the proportion of aggressive (hawk) individuals in the population and was compared to the case of the domestic cat population for which rural (low density) populations are mainly hawk and urban (high density) populations are mainly dove. However, in this previous model, the resource was assumed to be constant, i.e. at a constant level not depending for example on the predator density. The aim of this work is to take into account the interaction between the population and the resource in the frame of a predator–prey model. The resource is assumed to be a prey and the population is its predator.

The prey population grows logistically when not predated. Individual predators can use different tactics to get the resource. Predators can catch a prey and eat it, but they can also dispute a prey to another predator who has previously captured a prey. The aim of this work is to investigate the effects of individual tactics (hawk and dove) that can be used by predators on the overall stability of the predator–prey system. In a previous attempt (Auger et al., 2002) we presented such a model. In this contribution, we make explicit the process by which a predator manipulating a prey is found by a searching predator leading to a contest between the two predators. With respect to the previous work, we also incorporate a more realistic Holling type II functional response.

As in (Auger et al., 2002), we also considered two different time scales: a fast time scale corresponding to the hawk–dove game between predators and a slow time scale corresponding to prey growth and predator demography. The existence of two time scales was used to reduce the dimension of the model (a set of three ODES for the prey, hawk predator and dove predator densities) and to obtain an aggregated model that describes the dynamics of the total predator and prey densities at the slow time scale. For the aggregation methods we refer to (Bravo de la Parra et al., 1995; Auger and Poggiale, 1998; Bernstein et al., 1999; Auger and Bravo de la Parra, 2000).

In this article, we also incorporate searching and handling activities of the predators. The handling–searching processes shall occur at the fast time scale as well as the hawk–dove game. The resulting seven-dimensional complete model is reduced to a two-dimensional aggregated model.

The question that arises naturally in this model relates to the tactics that is the most favourable for predators. Should predators be aggressive and fight to monopolize the prey resource or should predators do not dispute preys with conspecifics occasioning fightings and resulting injuries? There is not a simple answer to this question. We show in this paper that it depends on the value of the cost.

In Neat et al. (1998a, b) the role of injury and energy metabolism during fights between male ciclid fish *Tilapia zillii* is studied experimentally. Both behavioural mechanisms underly the making of the strategic decisions in animal fighting. It is concluded that the injury data and energy metabolism data suggest that escalated fighting is costly for both winners and losers, but especially so for losers.

For the temporal change of the tactic, we will assume the classical replicator dynamics which together with the hawk–dove game model gives the well known predictions; when costs were lower than the gain a monomorphic hawk predator population, and a dimorphic predator population, when the costs are larger than the gain.

We will perform a full analysis of the aggregated models by presenting complete bifurcation analysis diagrams. The resulting model resembles the well known Rosenzweig–MacArthur predator–prey model (Rosenzweig, 1971) but its long term dynamics behaviour differs significantly. For the Rosenzweig–MacArthur model, we know that if the parameter values are such that an asymptotically stable interior equilibrium exists, then it is also globally stable (Hsu et al., 1978) and if such an equilibrium is unstable, a unique globally asymptotically stable limit cycle exists (Cheng, 1981). Similar to the Bazykin model (Kuznetsov, 1998; Bazykin, 1998), where in addition to the linear predator death rate term in the Rosenzweig–MacArthur model a quadratic death term for the predator is introduced, the dynamic behaviour of our model is more complex. A stabilizing effect is found due to mutual interference between the predators. This effect is similar to that found in the Beddington–DeAngelis predator–prey model, see Beddington (1975), DeAngelis et al. (1975).

The paper is organized as follows: First we present the complete model. Then we show that by use of aggregation methods, it is possible to build a global predator–prey model governing the total prey and predator densities, by total predator density we signify the predator density obtained by summation over all individual predator categories such as searching, handling, hawk and dove sub-populations. Thereafter, we present the results of the bifurcation analysis of the aggregated models with respect to two relevant parameters, the carrying capacity and the costs for fight. The article ends with a general discussion on advantages of different tactics and their effects on the stability of the predator–prey system.

2. Formulation of the model

This section is devoted to the introduction of the model. We take into account two types of processes. On the individual level, the model describes the behaviour of the predator individuals with respect to defending and fighting for food. On the population level, the model describes birth and death processes. We first explain the behavioural processes, then we describe the population processes. Finally, we build the complete model. It is a seven-dimensional system. The mathematical study is provided in the next section.

2.1. Behavioural model

On the individual level, predator individuals have three possible states of behaviour: they can be searching for prey, finding a prey or defending it. Individuals in each of these subpopulations can play the hawk or dove tactics. We denote by $p_{SD}, p_{FD}, p_{DD}, p_{SH}, p_{FH}$ and p_{DH} the biomass of searching and dove predators, finding and dove predators, defending and dove predators, searching and hawk predators, finding and hawk predators and defending and hawk predators, respectively. The individuals can change their tactics only in the defending subpopulation. Let

$$p_S = p_{SD} + p_{SH}, \tag{1a}$$

$$p_F = p_{FD} + p_{FH}, \tag{1b}$$

$$p_D = p_{DD} + p_{DH} \tag{1c}$$

be the biomass of searching predators, finding predators and defending predators, respectively.

Fig. 1 illustrates the fluxes between the six compartments. The fluxes between the subpopulation follow from mass-action arguments. For instance individuals (both posing the hawk and dove tactics) enter the finding subpopulation when they meet a prey individual and enter the defending subpopulation when they meet a finding predator individual. In the defending state the individuals can change their tactics via learning. The fluxes between the hawk and dove behaviours are given by the following gain matrix according to the hawk–dove model introduced in game theory (Hofbauer and Sigmund, 1998):

$$\mathbf{A} = \begin{array}{cc} DH & DD \\ \left(\begin{array}{c} \frac{G-C}{2} \\ 0 \end{array}\right. & \left.\begin{array}{c} G \\ \frac{G}{2} \end{array}\right) \end{array} \begin{array}{c} \\ DH \\ DD \end{array}, \tag{2}$$

where the pay-offs are to the individuals listed on the right when confronted with individuals listed above. The gain G of the game is the average amount of preys that two predators dispute per unit of time. When two hawks fight, they can get wounded. Let C be the cost due to fighting between hawks per a pair of defending predators and per unit of time. C is a positive parameter which is allowed to be larger than the gain G.

The hawk–dove game provides a simple characterization of contests between predators over a prey of value G. All predators are equal in their abilities, but may differ in terms of the behaviour that they adopt in a contest with another predator. A predator that plays hawk behaves aggressively and a predator that plays dove displays to the other predator and retreats if the other predator behaves aggressively.

Thus if a hawk contests the prey with a dove the hawk gets the prey. If two doves contest the prey they share it, each gets half the prey. If two hawks contest the prey they fight, one wins the other loses. The winner gets the prey and both winner and loser a cost that represents the loss in weight as a result of the injuries. At population level we say that each predator gets the half of the net gain that is $(G-C)/2$.

Let $\mathbf{u}$ be the vector $\mathbf{u} = ((p_{DH}/p_D), (p_{DD}/p_D))^{\mathrm{T}}$, where T denotes the transpose. We define $(\mathbf{Au})_D$ and $(\mathbf{Au})_H$ as follows:

$$(\mathbf{Au})_H = \frac{G-C}{2}\frac{p_{DH}}{p_D} + G\frac{p_{DD}}{p_D}, \tag{3a}$$

$$(\mathbf{Au})_D = \frac{G}{2}\frac{p_{DD}}{p_D}, \tag{3b}$$

where $(\mathbf{Au})_H$ (resp. $(\mathbf{Au})_D$) represents the average gain of a pure hawk (resp. dove) individual playing the hawk (resp. dove) tactic all the time against a population with given proportions (p_{DH}/p_D) of hawks and (p_{DD}/p_D) of doves. The average gain for the whole population reads

$$\mathbf{u}^{\mathrm{T}}\mathbf{Au} = \frac{p_{DH}}{p_D}(\mathbf{Au})_H + \frac{p_{DD}}{p_D}(\mathbf{Au})_D. \tag{4}$$

The proportions (p_{DH}/p_D) and (p_{DD}/p_D) change in time according to a behavioural model. Each predator learns the gain of another randomly chosen other predator and changes to the others tactic if he/she perceives that the other's gain is higher. However, information concerning the difference in the average gain of the two strategies is imperfect, so the larger the difference in the gains, the more likely the predator is to perceive it, and change. Based on these assumptions in Gintis (2000) the following equations are derived:

$$\frac{\mathrm{d}p_{DD}}{\mathrm{d}\tau} = c((\mathbf{Au})_D - \mathbf{u}^{\mathrm{T}}\mathbf{Au})p_{DD}, \tag{5a}$$

$$\frac{\mathrm{d}p_{DH}}{\mathrm{d}\tau} = c((\mathbf{Au})_H - \mathbf{u}^{\mathrm{T}}\mathbf{Au})p_{DH}, \tag{5b}$$

where c is a rate constant. These equations are called the *replicator dynamic* equations, After some algebraic

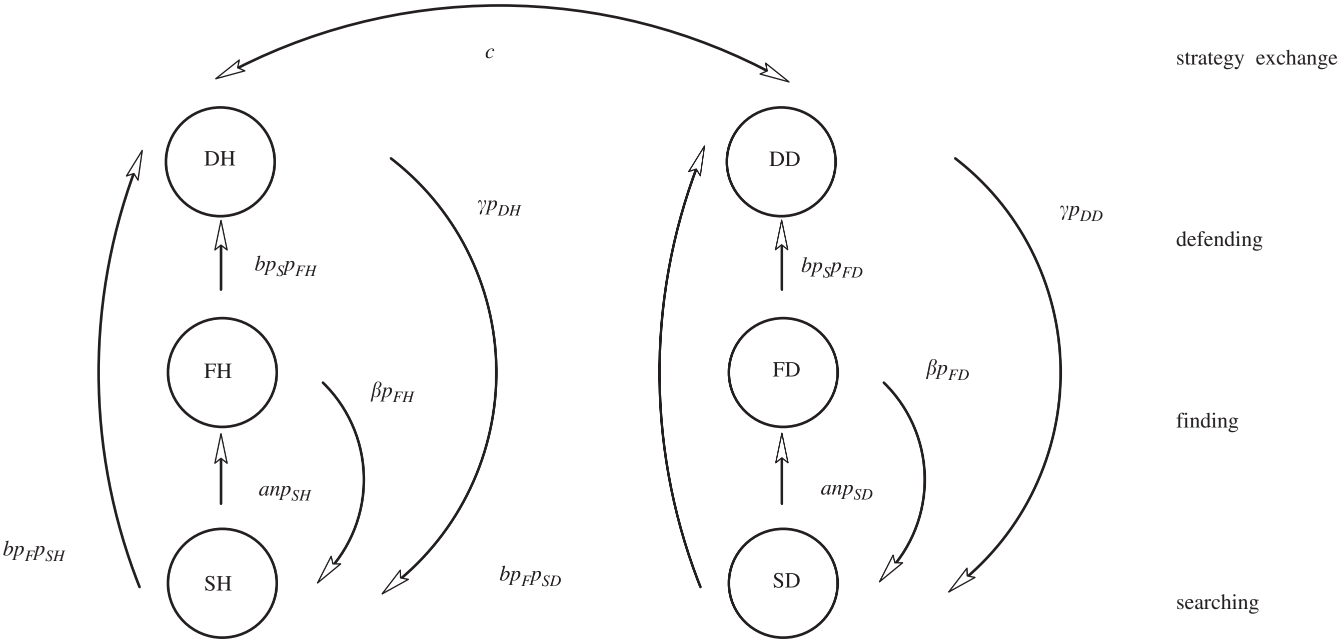

Fig. 1. The predator fluxes between the six compartments $p_{SD}, p_{SH}, p_{FD}, p_{FH}, p_{DD}, p_{DH}$. The fluxes except those between defending individuals are due to encounters between predator individuals in a different behaviour state or between a predator individual and a prey individual modelled by the law of mass-action. The fluxes between the two defending state model fluxes due to the change of tactics (hawk or dove) and these fluxes are modelled using the replicator equation. All fluxes change at the fast time-scale.

manipulations one obtains

$$\frac{\mathrm{d}p_{DD}}{\mathrm{d}\tau} = c\frac{p_{DH}}{p_D}\frac{p_{DD}}{p_D}((\mathbf{Au})_D - (\mathbf{Au})_H), \tag{6a}$$

$$\frac{\mathrm{d}p_{DH}}{\mathrm{d}\tau} = c\frac{p_{DH}}{p_D}\frac{p_{DD}}{p_D}((\mathbf{Au})_H - (\mathbf{Au})_D), \tag{6b}$$

where $c > 0$ is the proportional coefficient. The interpretation of Eqs. (6a) and (6b) is simple. Indeed, when the gain of the dove (resp. hawk) is greater than the gain of the hawk (resp. dove), the time derivative of Eq. (6) is positive (resp. negative) and thus the dove population (resp. hawk) increases. In other words, when a tactic leads to a better benefit than another, individuals switch to use it. Adding Eqs. (6a) and (6b) shows that the number of defending predator individuals $p_D = p_{DD} + p_{DH}$ does not change due to the fact that some individuals alter their tactics.

When the changes of behaviour for the predators individuals occur at the fast time scale, we have the following equations for the dynamics of the predator population:

$$\frac{\mathrm{d}p_{SD}}{\mathrm{d}\tau} = -bp_Fp_{SD} - anp_{SD} + \beta p_{FD} + \gamma p_{DD}, \tag{7a}$$

$$\frac{\mathrm{d}p_{FD}}{\mathrm{d}\tau} = -bp_Sp_{FD} + anp_{SD} - \beta p_{FD}, \tag{7b}$$

$$\begin{aligned}\frac{\mathrm{d}p_{DD}}{\mathrm{d}\tau} &= bp_Fp_{SD} - \gamma p_{DD} + bp_Sp_{FD} \\ &\quad + c((\mathbf{Au})_D - \mathbf{u}^{\mathrm{T}}\mathbf{Au})p_{DD},\end{aligned} \tag{7c}$$

$$\frac{\mathrm{d}p_{SH}}{\mathrm{d}\tau} = -bp_Fp_{SH} - anp_{SH} + \beta p_{FH} + \gamma p_{DH}, \tag{7d}$$

$$\frac{\mathrm{d}p_{FH}}{\mathrm{d}\tau} = -bp_Sp_{FH} + anp_{SH} - \beta p_{FH}, \tag{7e}$$

$$\begin{aligned}\frac{\mathrm{d}p_{DH}}{\mathrm{d}\tau} &= bp_Fp_{SH} - \gamma p_{DH} + bp_Sp_{FH} \\ &\quad + c((\mathbf{Au})_H - \mathbf{u}^{\mathrm{T}}\mathbf{Au})p_{DH},\end{aligned} \tag{7f}$$

where τ is the fast time scale. The parameter $a > 0$ is the prey–predator encounter rate for the predator, $\beta > 0$ is the rate of returning from handling a prey, $\gamma > 0$ is the rate of returning from handling a prey after dispute. The magnitude of the rates a, c, β and γ are such that all the terms on the right-hand side of the equations are of the same order.

In our model, after a predator catched a prey there is a time-window in which the predator can encounter another searching (both hawk and dove) predator. If it does, it enters the defending state in which it fights and thereafter handles the prey without interference with other predators. Both predator individuals become a searching predator after time $1/\gamma$. If it does not, the predator individual handles its prey without interference with other predators and enters the searching state $1/\beta$

after it found a prey. Hawk and dove predators have the same catch rate a.

We assume that each day predators capture a few preys. Therefore, at the fast time scale, predators are involved in the processes which are described in Fig. 1. A searching predator can capture a prey and it becomes a finding predator. If the finding predator is not found by another searching predator, it eats its prey completely and switches thereafter back to the searching state. Otherwise, if during its prey manipulation, the finding predator is encountered by another searching predator, both of them come into contest and switch to the defending state. In the defending state, their interaction is described by the hawk–dove game. Therefore, predators enter in contest at the same rate as they enter in the defending state, given by the expression bp_Sp_F (see Fig. 1). This expression represents the number of contests per unit of time which depends on the densities of searching and finding predators. At each contest, two defending predators dispute a single prey. Therefore, the prey biomass (assumed to be equal for all prey individuals) that pairs of defending predators dispute per unit of time is bp_Sp_F. As a consequence, a single defending predator disputes $bp_Sp_F/(p_D/2)$ leading to

$$G = 2\,\frac{bp_Sp_F}{p_D}, \tag{8}$$

which is the gain of the game, that is the prey biomass per unit of time that is obtained by a pair of defending predator. When there are many contests per unit of time, hawk predators fight more frequently and get more injured. Thus, in a similar way as for the gain, we assume that the per unit of time cost is proportional to the rate at which predators come into contest and consequently the cost per unit of time is proportional to the gain. Observe that the dimension of the gain and cost are per unit of time, since we consider the increased biomass of the predator due to ingestion of prey biomass per unit of time while the biomasses of the prey and predator are expressed in the same dimensions, for instance C-mole or grams.

At this stage we make some remarks. The predator–prey and predator–predator encounters occur at the individual level and we assume a well-mixed environment so that the law of mass-action is valid. Also fightings are between individuals. Hence the pay-offs are first formulated at the individual level. However, assuming large numbers of individuals allows us to use averages for the predator population of which the state is described by six biomass variables. Therefore, all rates, but also the gain and costs, are finally defined per predator biomass instead of per individual. Consequently, it is possible that although the gain shared by two disputing individuals is constant in (2), the average gain rate defined in (8) is time-dependent when the composition of the predator population changes in time. Later in the subsection we will show that in the fast equilibrium, this gain and also costs tend rapidly to a constant.

2.2. Predator–prey model

Let us now consider the temporal change of the total population biomasses. Firstly, we consider the prey dynamics. We assume a slow logistic growth for the prey in the absence of predator population. Furthermore, the prey are caught by searching predators. We assume that the loss of prey is proportional to the capture of prey, which, according to the mass-action law, is proportional to prey density and searching predator density. The model for the prey population reads

$$\frac{\mathrm{d}n}{\mathrm{d}\tau} = \varepsilon\left(rn\left(1-\frac{n}{K}\right) - ap_Sn\right), \tag{9}$$

where r is the intrinsic population growth rate, K is the carrying capacity and a is the prey–predator encounter rate for the prey. We assume that prey growth takes long periods of time (several weeks). Therefore, the logistic growth appears as a small term in Eq. (9). We thus introduce a small dimensionless parameter ε which is used to slow down the growth speed. Furthermore, we assume that the prey biomass which is captured per unit of time remains small. In other words, the prey biomass which is ingested per days remains small with respect to the total prey biomass. Thus, the predation term is also small in Eq. (9).

Secondly, we consider the predator population dynamics. Preys that are ingested by predators allow maintenance and growth. This is a slow process which takes long periods of time (several weeks) with respect to the day which is the time scale of prey captures. Prey biomass is used for maintenance of predators and is also converted into new predator biomass via reproduction. This conversion of prey biomass is assumed to occur slowly and we again use the small dimensionless parameter ε.

The predators in the finding state and in the defending state consume prey individuals and increase the predator population density. Two contributions must be considered, the flux of prey biomass corresponding to preys handled by finding predators and the flux of prey biomass that predators dispute in the defending state. They correspond to prey biomass ingested by predators and converted into predator biomass with some efficiency given by parameter α.

The predator population model is slow and reads as follows:

$$\frac{\mathrm{d}p_{SD}}{\mathrm{d}\tau} = \varepsilon(\alpha(\beta p_{FD} + (\mathbf{Au})_D p_{DD}) - \mu p_{SD}), \tag{10a}$$

$$\frac{\mathrm{d}p_{FD}}{\mathrm{d}\tau} = -\varepsilon\mu p_{FD}, \tag{10b}$$

$$\frac{dp_{DD}}{d\tau} = -\varepsilon\mu p_{DD}, \tag{10c}$$

$$\frac{dp_{SH}}{d\tau} = \varepsilon(\alpha(\beta p_{FH} + (\mathbf{Au})_H p_{DH}) - \mu p_{SH}), \tag{10d}$$

$$\frac{dp_{FH}}{d\tau} = -\varepsilon\mu p_{FH}, \tag{10e}$$

$$\frac{dp_{DH}}{d\tau} = -\varepsilon\mu p_{DH}, \tag{10f}$$

where α is the efficiency coefficient. The first contribution is the flux of prey biomass when hawk (resp. dove) predators return from finding to searching. These prey biomass fluxes are small, $\varepsilon\beta p_{FH}$ for hawks (resp. $\varepsilon\beta p_{FD}$ for doves). The second contribution corresponds to preys that are consumed by defending predators and is the prey biomass flux associated to the flux of predators entering the defending state from the searching and finding states, $(\mathbf{Au})_H p_{DH}$ for hawks (resp. $(\mathbf{Au})_D p_{DD}$ for doves). We recall that $(\mathbf{Au})_H$(resp. $(\mathbf{Au})_D$) represents the average prey biomass that hawk (resp. dove) defending predators eats per unit of time. Then, we must multiply by the number of predators of each type to obtain the total prey biomass ingested by the hawk and dove defending sub-populations.

We assume that the predators have a natural death rate μ at the slow time scale and that the slow predator increase of biomass which is due to prey consumption only occurs in the searching state.

The complete model is obtained by coupling the previous predator behavioural model and the populations model as follows:

$$\begin{aligned}\frac{dp_{SD}}{d\tau} = & - bp_F p_{SD} - anp_{SD} + \beta p_{FD} + \gamma p_{DD} \\ & + \varepsilon(\alpha(\beta p_{FD} + (\mathbf{Au})_D p_{DD}) - \mu p_{SD}),\end{aligned} \tag{11a}$$

$$\frac{dp_{FD}}{d\tau} = -bp_S p_{FD} + anp_{SD} - \beta p_{FD} - \varepsilon\mu p_{FD}, \tag{11b}$$

$$\begin{aligned}\frac{dp_{DD}}{d\tau} = & \, bp_F p_{SD} - \gamma p_{DD} + bp_S p_{FD} \\ & + cp_{DD}((\mathbf{Au})_D - \mathbf{u}^{\mathrm{T}}\mathbf{Au}) - \varepsilon\mu p_{DD},\end{aligned} \tag{11c}$$

$$\begin{aligned}\frac{dp_{SH}}{d\tau} = & - bp_F p_{SH} - anp_{SH} + \beta p_{FH} + \gamma p_{DH} \\ & + \varepsilon(\alpha(\beta p_{FH} + (\mathbf{Au})_H p_{DH}) - \mu p_{SH}),\end{aligned} \tag{11d}$$

$$\frac{dp_{FH}}{d\tau} = -bp_S p_{FH} + anp_{SH} - \beta p_{FH} - \varepsilon\mu p_{FH}, \tag{11e}$$

$$\begin{aligned}\frac{dp_{DH}}{d\tau} = & \, bp_F p_{SH} - \gamma p_{DH} + bp_S p_{FH} \\ & + cp_{DH}((\mathbf{Au})_H - \mathbf{u}^{\mathrm{T}}\mathbf{Au}) - \varepsilon\mu p_{DH},\end{aligned} \tag{11f}$$

$$\frac{dn}{d\tau} = \varepsilon\left(rn\left(1 - \frac{n}{K}\right) - anp_S\right). \tag{11g}$$

3. The aggregation method

We deal with the seven-dimensional system (11), by means of the aggregation method. We take advantage of the two time scales to reduce the dimension of the complete previous system of seven equations into a system of two equations only. For aggregation methods, we refer to Iwasa et al. (1987, 1989), Auger and Bravo de la Parra (2000), Bravo de la Parra et al. (1995). They permit to reduce the study to a two-dimensional system governing the total population variables n and p. Indeed, these variables are slow, that is they almost do not change on the fast processes time scale. Consequently, the total population dynamics governed by the aggregated model and the complete model are ε close. Thus we analyze the system by considering n and p as constant and we show that the remaining system has a stable fast equilibrium. Then we replace the fast variables by their equilibrium values in the n and p derivatives equations. The obtained model is called "aggregated model" and is analyzed in the next section.

3.1. Fast equilibrium

Using the fast system (7) one can build a three-dimensional system governing the variables p_S, p_F and p_D. This system reads

$$\frac{dp_S}{d\tau} = -bp_F p_S - anp_S + \beta p_F + \gamma p_D, \tag{12a}$$

$$\frac{dp_F}{d\tau} = -bp_S p_F + anp_S - \beta p_F, \tag{12b}$$

$$\frac{dp_D}{d\tau} = 2bp_F p_S - \gamma p_D. \tag{12c}$$

Notice that the sum of the three equations in (12) is null. Indeed, the total number of predators is not affected by the change of behaviour of individuals. As a consequence, we can omit one equation by considering the total number of predators $p = p_S + p_F + p_D$. We replace p_D by $p - p_S - p_F$ in Eqs. (12a, b). We thus get the following set of differential equations:

$$\frac{dp_S}{d\tau} = -bp_F p_S - anp_S + \beta p_F + \gamma(p - p_S - p_F), \tag{13a}$$

$$\frac{dp_F}{d\tau} = -bp_S p_F + anp_S - \beta p_F. \tag{13b}$$

At equilibrium, both equations are vanishing. Let p_S^*, p_F^* and p_D^* denote the equilibrium values of the variables. By using the second equation, we get the following relation:

$$p_F^* = \frac{an}{\beta + bp_S^*}\, p_S^*. \tag{14}$$

We then substitute this expression for p_F in the right-hand side of Eq. (13a) and put it equal to zero since we are interested in the equilibria of the fast system. We get

$$p_S^* = \frac{\gamma(bp - \beta - an) + \sqrt{\gamma^2(bp - \beta - an)^2 + 8ab\gamma\beta np + 4\gamma^2\beta bp}}{2(2abn + b\gamma)}. \tag{15}$$

Finally, we have

$$p_D^* = p - p_S^* - p_F^*. \tag{16}$$

Now, let us denote by p_{SD}^*, p_{FD}^*, p_{DD}^*, p_{SH}^*, p_{FH}^*, p_{DH}^* the equilibrium values associated to the fast system, obtained by letting $\varepsilon = 0$ in the previous seven-dimensional system (7) and let $t = \varepsilon\tau$.

At the fast equilibrium, a simple calculation shows that $G^* = \gamma$. In the same way we denote the costs at the fast equilibrium by $C^* = \delta$. Since we have constant equilibrium of the fast system, the gain is constant and equals the return rate from the defending state to the searching state. In a similar way also the costs δ are constant.

It remains to determine the equilibrium values p_{SD}^*, p_{FD}^*, p_{DD}^*, p_{SH}^*, p_{FH}^*, p_{DH}^*. It is easy to check that this equilibrium state is reached at the same conditions that are needed by the defending subpopulations to reach the game dynamics equilibrium of system (6). That is, the fast game dynamics, $p_{DH} \Leftrightarrow p_{DD}$, is decoupled from the fast predator composition dynamics, $p_{SH} \Leftrightarrow p_{FH} \Leftrightarrow p_{DH}$ and $p_{SD} \Leftrightarrow p_{FD} \Leftrightarrow p_{DD}$. We obtain for p_{DH}^* and p_{DD}^*

$$p_{DH}^* = \frac{\gamma}{\delta}\, p_D^*, \quad p_{DD}^* = \frac{\delta - \gamma}{\delta}\, p_D^*. \tag{17}$$

Hence, there is only a positive nontrivial equilibrium when $\gamma < \delta$. This is the dimorphic case where the predator population consists of hawk and dove predators. There are also the two trivial equilibria, the monomorphic cases, $(p_{DH}^*, p_{DD}^*) = (0, p_D^*)$ (only doves) and

$$p_{DH}^* = p_D^*, \quad p_{DD}^* = 0 \tag{18}$$

(only hawks). It is easy to show that: if $\gamma < \delta$, then the nontrivial equilibrium is stable and the other ones are unstable, while if $\gamma > \delta$ then the nontrivial becomes unstable and the trivial equilibrium $(p_{DH}^*, p_{DD}^*) = (p_D^*, 0)$ becomes stable.

The equilibrium values for the other variables can be calculated with the following formulas:

$$p_{FD}^* = \frac{an\gamma}{(bp_S^* + \beta)(bp_F^* + an) - an\beta}\, p_{DD}^*, \tag{19a}$$

$$p_{SD}^* = \frac{\beta p_{FD}^* + \gamma p_{DD}^*}{bp_F^* + an}, \tag{19b}$$

$$p_{FH}^* = \frac{an\gamma}{(bp_S^* + \beta)(bp_F^* + an) - an\beta}\, p_{DH}^*, \tag{19c}$$

$$p_{SH}^* = \frac{\beta p_{FH}^* + \gamma p_{DH}^*}{bp_F^* + an}. \tag{19d}$$

Observe that the denominators are positive and therefore also the biomasses of the subpopulations. In Appendix A, we show that this equilibrium of the six-dimensional fast system (7) is hyperbolically stable; a requirement for applying the aggregation technique.

3.2. *The aggregated model*

We build the population model where we use time-scale arguments. The derivative of the total predator population $p = p_{SD} + p_{FD} + p_{DD} + p_{SH} + p_{FH} + p_{DH}$ equals

$$\frac{\mathrm{d}p}{\mathrm{d}t} = \alpha(\beta p_F + (\mathbf{Au})_H p_{DH} + (\mathbf{Au})_D p_{DD}) - \mu p, \tag{20}$$

here we use the fact that $1/\beta$ is the handling time and the definition of the gain of the hawk–dove game.

A straightforward calculation shows that the equations for the total populations densities can be rearranged as follows:

- If $\gamma < \delta$ then we have the dimorphic case (mixed hawk and dove predators) which we call model I:

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rn\left(1 - \frac{n}{K}\right) - anp_S^*, \tag{21a}$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = -\mu p + \alpha\left(\beta p_F^* + \frac{\gamma}{2}\left(1 - \frac{\gamma}{\delta}\right)p_D^*\right). \tag{21b}$$

- If $\gamma > \delta$ then we have the monomorphic case (only hawk predators) which we call model II:

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rn\left(1 - \frac{n}{K}\right) - anp_S^*, \tag{22a}$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = -\mu p + \alpha\left(\beta p_F^* + \frac{\gamma}{2}\left(1 - \frac{\delta}{\gamma}\right)p_D^*\right), \tag{22b}$$

  where the values of p_S^*, p_F^* are given by (14,15) and $p_D^* = p - p_S^* - p_F^*$. Observe that the switch between the models when $\gamma = \delta$ is smooth with respect to the state variables $n(t)$ and $p(t)$.

After this two-dimensional system has been solved, approximations for the densities of the various subpopulations $p_{SD}(t), p_{FD}(t), p_{DD}(t), p_{SH}(t), p_{FH}(t), p_{DH}(t)$ can be calculated, according to the quasi-steady state assumption, with Eqs. (17)–(19).

4. Bifurcation analysis of the aggregated model

We present bifurcation diagrams for the aggregated model, two-parameter bifurcation diagram Fig. 2 and one-parameter bifurcation diagrams (Figs. 3 and 4). The bifurcation diagrams were calculated using the software packages AUTO (Doedel et al., 1997), LOCBIF (Khibnik et al., 1993; Kuznetsov, 1998).

In a one-parameter bifurcation diagram Fig. 3 the biomass of the prey (bottom panel) and predator (top panel) are plotted as a function of the free parameter δ while other parameters are fixed at values given, while $K=10$. Stable equilibria are presented by a solid line and unstable equilibria by a dashed line in which case there is a limit cycle that surrounds the unstable equilibrium. The maximum and minimum values during one period are plotted as solid lines when the limit cycle is stable and dashed lines when it is unstable (this latter case does not occur for $K=10$).

For intermediate δ values in a range around the value $\delta=\gamma=1$ bounded by supercritical Hopf bifurcations H^- for each model, the positive equilibrium is stable. Outside this range for low and high δ values the solution oscillates. In this cyclic regime the minimum of the prey population becomes very low and extinction due to stochastic effects becomes likely.

In Fig. 4 a similar plot is given, where $K=20$. Again the equilibrium is unstable for low and high δ-values. The Hopf bifurcations are however of a different nature than those for $K=10$ given in Fig. 3. Here the Hopf bifurcations, for each model, are subcritical denoted by H^+. For instance for increasing δ this means that the originating limit cycle is unstable and close to the Hopf bifurcation there are two attractors a stable equilibrium and a stable limit cycle. This stable limit cycle emanates from a tangent bifurcation of the limit cycle, denoted by T_c, where a stable and an unstable limit cycle coincide.

So, for $K=10$ there are two supercritical Hopf bifurcations H^- and for $K=20$ two subcritical Hopf bifurcations H^+. Hence there is an intermediate critical K-value where the Hopf bifurcations change nature. The critical points are codim-two Bautin bifurcation points. These points are denoted by B in the two-parameter bifurcation diagram (Fig. 2) where δ and K act as bifurcation parameters. The tangent bifurcation of the limit cycle, denoted by T_c, originates in this point (Fig. 2).

Below the transcritical bifurcation curve TC the predator cannot invade the prey population for the carrying capacity K is too low to support both prey and predator population.

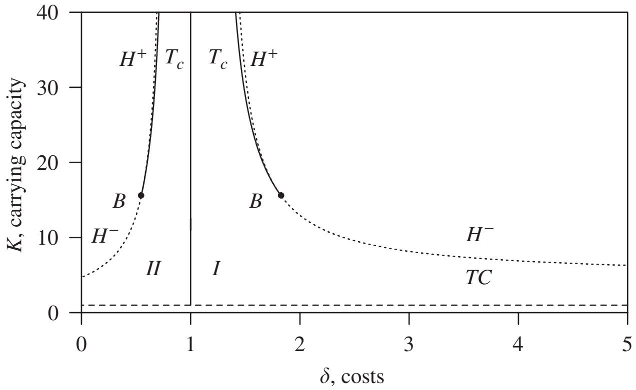

Fig. 2. The two-dimensional bifurcation diagram for the aggregated system using δ and K as bifurcation parameters. The transcritical bifurcation (TC) marks the region of coexistence for K values above this curve. Two supercritical Hopf bifurcations (H^-) mark regions where the system cycles. Parameters: $r=1.0$, $b=1.0$, $\beta=1.0$, $\gamma=1.0$, $a=1.0$, $\alpha=1.0$ and $\mu=0.5$. The solid vertical curve separates the regions where models I and II apply.

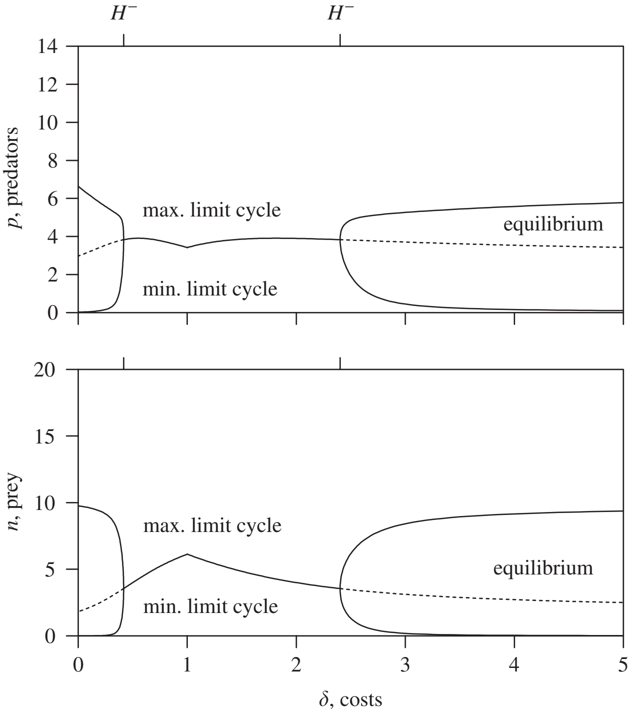

Fig. 3. One-parameter diagram of the prey (bottom) predator (top) biomasses, n and p respectively, with δ as bifurcation parameter and $K=10$. This point is below the Bautin bifurcation point B where the positive equilibrium becomes unstable at a supercritical Hopf H^-, where stable oscillations occur. For these limit cycles the maximum and minimum values are plotted.

5. Discussion and conclusions

We stress that although the equations of the behavioural part are the same as those in the classical hawk–dove contest in evolutionary theory, the interpretations of the various terms here differ. In the classical hawk–dove contests, see for instance (Hofbauer and Sigmund, 1998), the gain is the increase in fitness,

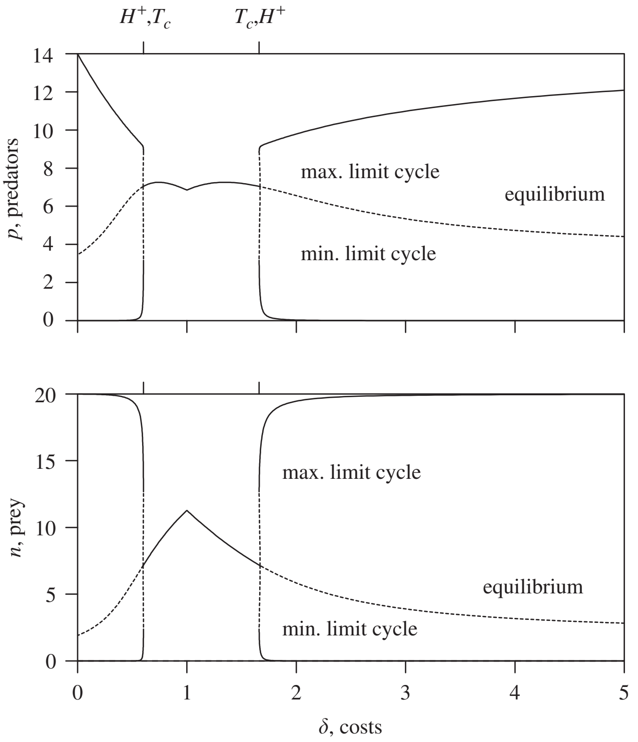

Fig. 4. One-parameter diagram of the prey (bottom) predator (top) biomasses, n and p respectively, with δ as bifurcation parameter and $K = 20$. This point is above the point B where the positive equilibrium becomes unstable at a subcritical Hopf bifurcation H^+ where unstable oscillations occur. These unstable limit cycles become stable in a tangent bifurcation point for limit cycles, denoted by T_c. For these limit cycles the maximum and minimum values are plotted (solid: stable and dashed: unstable).

here it is the increase in predator-biomass due to the consumption of prey-biomass. In the classical hawk–-dove game the rate of change of the tactics (on the evolutionary time-scale) is small with respect to the predator–prey development rate (ecological time-scale), here the rates in the replicator equations are fast just as the predator–prey interaction rate in the Holling disc-equation with respect to the predator–prey development rate. In the classical hawk–dove game mutants invade the resident strategies and cause an evolutionary sequence to an evolutionary endpoint, here the defending predator individuals learn and switch tactics fast, possibly many times during their lifetime.

For the growth of the prey we use the logistic equation which is a basic paradigm in population ecology, introduced in almost any textbook on ecology. In Kooi et al. (1997, 1998b) it is argued that when the prey consumes a nutrient and is consumed itself by a predator the law of mass conservation is not obeyed. However, the resulting model is three dimensional. In this article we concentrate on the effects of behavioural aspects in the predator–prey interaction on the dynamics and for the sake of simplicity we assumed logistic growth of the prey. The resulting model is two-dimensional and this simplifies the analytical treatment. Numerical bifurcation analysis in combination with aggregation techniques for a fast–slow predator–prey-nutrient system under batch and chemostat environmental conditions without recycling is performed in Kooi et al. (1998a, 2002) for the case when nutrient recycling is possible.

Let us say a few words about the structure and meaning of the aggregated models. Therefore, we consider the limiting case $b \to 0$. The quadratic equation for p_S has the following positive solution

$$p_S^* = \frac{\beta p}{\beta + an}, \tag{23}$$

when $b \to 0$. Furthermore, we have

$$p_F^* = p - p_S^* = \frac{anp}{\beta + an} = \frac{an}{\beta} p_S^*, \quad p_D^* = 0. \tag{24}$$

Hence, the limiting case $b = 0$ yields indeed the classical Rosenzweig–MacArthur model with the Holling type II functional response for the trophic interaction between the predator and prey population. The aggregated model (21), (22), reads

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rn\left(1 - \frac{n}{K}\right) - anp_S^*, \quad \frac{\mathrm{d}p}{\mathrm{d}t} = -\mu p + \alpha\beta p_F^*, \tag{25}$$

or

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rn\left(1 - \frac{n}{K}\right) - \frac{\beta anp}{\beta + an}, \quad \frac{\mathrm{d}p}{\mathrm{d}t} = -\mu p + \alpha\frac{\beta anp}{\beta + an}. \tag{26}$$

For this Rosenzweig–MacArthur model, the paradox of enrichment holds and for large values of the carrying capacity K of the prey, the equilibrium becomes unstable and a stable limit cycle occurs. In the general case when $b \neq 0$, the bifurcation diagram shows that in a given cost range, there is a stable equilibrium point with constant prey and predator biomasses. For example, if the cost δ is set close to $\gamma = 1$, then an increase of the carrying capacity K of the prey does not lead to oscillations of prey and predator biomasses. Therefore, in this range of costs, the paradox of enrichment is not observed. In this range, the prey–predator system is stable. This can occur for a pure hawk predator population, corresponding to model I, where costs should be limited (smaller than the gain). Therefore, to have global stability, fightings between hawks should not involve too much injuries. However, stability can also occur for a mixed hawk–-dove predator population, corresponding to model II, for a cost close but smaller than the return rate. Therefore, it turns out that the behavioural interactions between the defending predators has a stabilizing effect on the prey–predator system. This is in agreement with the findings in DeAngelis et al. (1975) where it is stated that: "mutual interference between the predators is a major stabilizing factor in a nonlinear system."

The bifurcation diagram also shows that for small and large cost values, the paradox of enrichment is observed with a stable equilibrium at small prey carrying capacity and a stable limit cycle for larger ones. However, due to the existence of a Bautin bifurcation which is never possible in the classical Rosenzweig–MacArthur model, there exists a narrow area of cost values in which a stable equilibrium and a stable limit cycle separated by the stable manifold of the unstable limit cycle can co-occur. Therefore, according to initial conditions, the prey and predator populations can coexist at constant biomasses or cycle.

We also studied the bifurcation diagrams for different values for the other parameters, for example b. We found that the bifurcation pattern is robust for reasonable ranges of these parameters around the reference values mentioned in the caption of Fig. 2.

Appendix A. Stability of the fast system

The Jacobian matrix evaluated at the equilibrium (p_S^*, p_F^*) of the two-dimensional system for the state variable (p_S, p_F) reads

$$\mathbf{J} = \begin{pmatrix} -bp_F^* - an - \gamma & -bp_S^* + \beta - \gamma \\ -bp_F^* + an & -bp_S^* - \beta \end{pmatrix}. \tag{27}$$

Clearly, the trace of this matrix is negative. The determinant reads

$$\begin{aligned} \det(\mathbf{J}) &= \beta bp_F^* + 2abnp_S^* + \gamma bp_S^* + \gamma\beta + \beta bp_F^* \\ &\quad - \gamma bp_F^* + \gamma an \\ \det(\mathbf{J}) &> -\gamma bp_F^* + \gamma an = \gamma(an - bp_F^*). \end{aligned} \tag{28}$$

Now, at equilibrium, (13b) is equivalent (if $p_S^* \neq 0$) to

$$an - bp_F^* = \beta \frac{p_F^*}{p_S^*} > 0, \tag{29}$$

and hence the determinant is positive. Therefore, both eigenvalues of the Jacobian matrix are negative or have negative real part. This shows that the equilibrium (p_S^*, p_F^*), given in (15), is stable for the system (13).

With (16) the solution of the three-dimensional system (12) converges to the equilibrium (p_S^*, p_F^*, p_D^*), where p_D^* is given in (15), after a small perturbation.

The equilibria (p_{DH}^*, p_{DD}^*) are those of replicator equations (6), where $p_D^* = p_{DD}^* + p_{DH}^*$ is given in (15). The equilibrium values are given by (17) and (18) when $\gamma < \delta$ and $\gamma > \delta$ respectively. This equilibrium of the replicator system (6) which is decoupled from the other elements of the complete fast system (7) is stable.

By definition (1) we have $p_S = p_{SD} + p_{SH}$. So, the sum of the searching hawk and dove predator biomasses p_S converges to its equilibrium state after small perturbations from (p_S^*, p_F^*, p_D^*). However, both p_{SD} and p_{SH} do not need to converge to their equilibrium values separately, only their sum does. The same holds for the finding predators $p_F = p_{FD} + p_{FH}$. Therefore we analyze the complete fast system.

The six-dimensional fast system (7) reads

$$\frac{\mathrm{d}p_{SD}}{\mathrm{d}\tau} = -bp_F^* p_{SD} - anp_{SD} + \beta p_{FD} + \gamma p_{DD}^*, \tag{30a}$$

$$\frac{\mathrm{d}p_{FD}}{\mathrm{d}\tau} = -bp_S^* p_{FD} + anp_{SD} - \beta p_{FD}, \tag{30b}$$

$$0 = bp_F^* p_{SD} - \gamma p_{DD}^* + bp_S^* p_{FD}, \tag{30c}$$

$$\frac{\mathrm{d}p_{SH}}{\mathrm{d}\tau} = -bp_F^* p_{SH} - anp_{SH} + \beta p_{FH} + \gamma p_{DH}^*, \tag{30d}$$

$$\frac{\mathrm{d}p_{FH}}{\mathrm{d}\tau} = -bp_S^* p_{FH} + anp_{SH} - \beta p_{FH}, \tag{30e}$$

$$0 = bp_F^* p_{SH} - \gamma p_{DH}^* + bp_S^* p_{FH}, \tag{30f}$$

where (p_S^*, p_F^*, p_D^*) and (p_{DH}^*, p_{DD}^*) are the equilibria of the decoupled subsystems.

Eq. (30c) gives

$$bp_F^* p_{SD} + bp_S^* p_{FD} = \gamma p_{DD}^*, \tag{31}$$

where p_{DD}^* is given in (18). Substitution of the expression for p_{FD} into (30a) yields

$$\frac{\mathrm{d}p_{FD}}{\mathrm{d}\tau} = -(bp_S^* + an\frac{p_S^*}{p_F^*} + \beta)p_{FD} + \frac{an\gamma p_{DD}^*}{bp_F^*}. \tag{32}$$

Because of the negative rate, small perturbations of p_{FD} from its equilibrium (19a) diminishes exponentially. Then, since $p_F^* = p_{FD} + p_{FH}$, also p_{FH} returns to its equilibrium value (19d) after a small perturbation. Similarly one can show that this holds also for p_{SD} and p_{SH}. We conclude using the special case of Theorem 1.1 mentioned on page 316 in Coddington and Levinson (1955) that the equilibrium of the fast system is stable.

This allows application of the aggregation techniques, see Sakamoto (1990).

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