



Effect of aggressive behaviour on age-structured population dynamics

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Abstract

In this work, we present an age-structured population model that incorporates individual behaviour. A classical Leslie matrix model is used to describe the population demography. Adults acquire resources required to survive and reproduce by using two contrasted behavioural tactics (hawk versus dove). Individual survival depends on the average cost of fights while individual fecundity depends on the average gain in the competition to access the resource. We investigated variation in fecundity according to the amount of resources available by using two functions: a Holling type function and a threshold function. We aimed to assess the long-term effects of conflicting tactics of resource acquisition on population dynamics. Our model includes two parts: a fast part that describes the encounters and fights involves a game dynamic model based upon the replicator equations in discrete time; and a slow part that describes the long-term effects of conflicting tactics on the population growth rate. The use of aggregation methods allowed us to reduce the proposed initial model into an aggregated model that describes the dynamics of the population (a Leslie matrix model). We analysed the effects of gain and cost parameters on the asymptotic growth rate of the total population. © 2005 Elsevier B.V. All rights reserved.

Keywords: Game dynamics; Leslie model; Aggregation methods; Individual behaviour; Aggressiveness

1. Introduction

Studying the consequences of the variation in individual behaviour on population dynamics and stability of communities is one of the major task the ecologists face (Sibly, 1985; Lomnicki, 1980). Indeed a considerable amount of phenotypic plasticity occurs among and

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within populations, in particular for behavioural traits (Lott, 1991; Stamps and Buechner, 1985). The ability for an individual to survive and reproduce depends on its behaviour (Krebs and Davies, 1993). Individuals compete for resources (such as mate, within the habitat, intraspecific competition is expected to increase. In that case, we can expect that individuals will develop behavioural tactics according to their phenotypic quality in order to maximize food acquisition (Manning and Dawkins, 1998). This has recently led to the concept of behaviour-based models (Sutherland and Norris, 2002).

Here, we present an approach aimed to link individual variation in behaviour and population dynamics. By coupling a game model that describes interactions among individuals (Maynard Smith, 1982; Sigmund, 1986; Hofbauer and Sigmund, 1988; Cressman, 1992; Mesterton-Gibbons, 1992) quite similar to the game model used by Auger et al. (1998), Auger and Pontier (1998), and Sanchez et al. (1997) with a model that describes population growth (a Leslie matrix). We consider a population in which individuals compete for a given resource that is required to survive and/or reproduce. To gain access to this resource, individuals display different behavioural tactics. We consider that individuals can use two different tactics: aggressive (hawk) or non-aggressive (dove) (Hofbauer and Sigmund, 1988; Maynard Smith, 1982). The hawk is aggressive and fights in any case, whereas the dove never does. When a hawk meets a dove, he wins. When two hawks meet, they fight and risk injuries, which may cause the death of one of them. When two doves meet, they do not fight: one of them retreats and the other one has access to the resource.

We assume that the demographic process, the growth of the population, acts at a slow-time scale in comparison with the encounters and fights (Auger and Bravo de la Parra, 2000; Bravo de la Parra et al., 1995). At the fast-time scale, individuals encounter and fight, the winners of the game obtain a reward G , which represents an access to a resource.

In our model, we assume that during its lifetime, an individual experiences several contests and is capable of learning and to adopt the strategy, which leads to the best payoff. This corresponds to the concept of behavioural plasticity. Individuals can modify their behaviour at a fast-time scale.

Demography corresponds to reproduction and mortality, which are assumed to occur at a slower time scale. Fecundity and survival usually depend on resource availability (Begon et al., 1996). The abundance of the resource is expected to modify the intensity of the competition among individuals. Therefore, we also included in our model the dependence of both fecundity and survival on the average gain and cost of the game in the long term.

As two time scales are involved in the dynamics, we can use aggregation methods to build a reduced model (the aggregated model) that describes the dynamics of the total population at the slow-time scale (Iwasa et al., 1987; Auger and Bravo de la Parra, 2000).

We first present the complete model for one population and two tactics (hawk and dove). The mathematical model is based upon the game dynamic model (the fast part) and the classical Leslie model (the slow part). We then present the construction of the so-called aggregated model. Next, we analyse the aggregated model by using two cases (a continuous versus a doorway effect). The last sections are devoted to the interpretation of the results and general conclusions.

2. The model

We consider a population including two categories of individuals: aggressive (hawk) or non-aggressive (dove). Individuals are assumed to compete to access resources.

The population is age-structured with two age-classes. One-year-old individuals (juveniles) do not participate to reproduction. Adult reproductive individuals (2 years old and older) are split between hawks and doves. The total population vector is thus:

$$\mathbf{N}(t) = (n_1(t), n_H(t), n_D(t))^T \quad (1)$$

where $n_1(t)$ is the number of individuals of age 1; $n_H(t)$ the number of Hawks (age 2 and older); $n_D(t)$ the number of Doves (age 2 and older) and T denotes the transposition. The number of individuals aged 2 and older is:

$$\mathbf{n}_2(t) = n_H(t) + n_D(t) \quad (2)$$

The complete model is the combination of two sub-models and takes into account two time scales. It is written as follows (Bravo de la Parra et al., 1995):

$$\mathbf{N}(t + 1) = \mathbf{L}\mathbf{J}^k\mathbf{N}(t) \tag{3}$$

where k is an integer which needs to be much larger than 1: $k \gg 1$.

The time step of the complete model is one year. \mathbf{L} is a Leslie matrix which describes the survival and fecundity processes (Caswell, 2001). \mathbf{J} is a game matrix describing hawk–dove interactions between competing individuals. The game matrix is frequency dependent (see below). By \mathbf{J}^k , we mean that the game sub-model is composed with itself k times, i.e. $\underbrace{J \times J \times J \times \dots \times J}_k$.

According to the previous assumption, two different time scales are involved, a fast one corresponding to hawk–dove interactions and a slow one corresponding to the demographic process.

2.1. The hawk–dove sub-model

We used the hawk–dove game model with discrete time. Individuals in this population can use hawk (H) and dove (D) tactics. The winner of the game gains an access to a common resource. Therefore, we assume that the gain G is identical for all individuals. C is the cost of loosing an escalated fight. The payoff obtained by hawks and doves when interacting are represented by the classical payoff matrix \mathbf{A} (Hofbauer and Sigmund, 1988):

$$\mathbf{A} = \begin{pmatrix} H & D \\ \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix} \begin{matrix} H \\ D \end{matrix} \tag{4}$$

The hawk–dove model is classical and for more details we refer to standard books (Maynard Smith, 1982; Hofbauer and Sigmund, 1988; Cressman, 1992). It can be shown that if $G > C$, there exists a positive pure hawk stable equilibrium, $n_H^* = n_2$ and $n_D^* = 0$ while if $G < C$, there exists a positive mixed stable equilibrium, $n_H^* = (\frac{G}{C})n_2$ and $n_D^* = (1 - \frac{G}{C})n_2$ (Hofbauer and Sigmund, 1988; Cressman, 1992).

Let \mathbf{J} be the frequency dependent evolutionary game matrix.

2.2. The Leslie submodel

The Leslie matrix (\mathbf{L}) is written as follows:

$$\mathbf{L} = \begin{pmatrix} 0 & F_H & F_D \\ qS_1 & S_H & 0 \\ (1-q)S_1 & 0 & S_D \end{pmatrix} \tag{5}$$

F_H and F_D are the fecundities of individuals aged 2 and more, respectively, for hawk and dove subgroups. S_H and S_D are the yearly survival of individuals aged 2, respectively, for hawk and dove subgroups. Parameter q represents the proportion of juveniles becoming hawk when surviving to adult (respectively $(1 - q)$ for dove). If we assume that an adult produces offspring who have the identical behaviour, then q should be equal to n_H/n_2 . If we assume that new adults are equally distributed between hawk and dove, q should be equal to $1/2$. S_1 is the survival of individuals from juvenile to adult which is assumed to be the same for hawk and dove.

2.2.1. Survival

We assume that escalated contests cause injuries and therefore provoke a decrease of the yearly survival of adult individuals according to the following relation: $S_i = Se^{\alpha \bar{C}_i}$, where \bar{C}_i is the average cost received by an individual of sub-group i , $i = H, D$ and α a positive coefficient which permits to regulate the effect of the average cost on the survival. α is a parameter related to environmental conditions.

The average cost is calculated by adding the cost of each type of encounter weighted by the proportion of this type of encounter. Therefore, the average cost received by a dove, that we note \bar{C}_D is null, because doves do not fight and do not get injured:

$$\bar{C}_D = 0 \frac{n_H}{n_2} + 0 \frac{n_D}{n_2} = 0 \tag{6}$$

As a consequence, dove survival (S_D) is simply S :

$$S_D = S \tag{7}$$

On the contrary, hawks fight and get injured which causes them higher mortality risks than doves. Hawk survival is a function of the average cost received by a hawk, that we note \bar{C}_H :

$$\bar{C}_H = \left(\frac{C}{2}\right) \frac{n_H}{n_2} + 0 \frac{n_D}{n_2} = \left(\frac{C}{2}\right) \frac{n_H}{n_2}, \tag{8}$$

The hawk survival (S_H) is thus given by the following expression:

$$S_H = Se^{\frac{\alpha C n_H}{2n_2}}, \tag{9}$$

2.2.2. Fecundity

For some species, the amount of resource has a continuous effect on fecundity, while for others, individuals must accumulate a given amount of resource before reproduction. We are going to assume that fecundity depends on average gains \bar{G}_i , $i=H, D$. Average gains are calculated by adding the gain of each type of encounter weighted by the proportion of this type of encounter. Thus, we obtain the next expressions for hawk (H) and dove (D) average gains:

$$\bar{G}_H = \left(\frac{G}{2}\right) \frac{n_H}{n_2} + G \frac{n_D}{n_2} \tag{10}$$

$$\bar{G}_D = 0 \frac{n_H}{n_2} + \left(\frac{G}{2}\right) \frac{n_D}{n_2} = \left(\frac{G}{2}\right) \frac{n_D}{n_2} \tag{11}$$

Let $F_2(\bar{G})$ be the fecundity function of the average gain for adults aged 2 and older.

2.2.2.1. Holling type fecundity function. First, in order to study the effect of the resource on fecundity, we use a Holling type function. According to this function, fecundity increases with the average gain and then reaches a plateau. Thus, we choose the following gen-

eral relationship between fecundity and average gain:

$$F_2(\bar{G}) = F \frac{\bar{G}}{\gamma + \bar{G}} \tag{12}$$

We use the average gains of Hawk and Dove of Eqs. (10) and (11) to calculate their respective fecundities. Fecundity is an increasing function of the average gain. Parameter γ permits to influence the “speed” to reach the plateau of the fecundity. When γ decreases the maximum of the fecundity is reached more quickly. γ translates the effect of poor environmental conditions on the fecundity.

2.2.2.2. Fecundity function with a threshold effect.

For some species, the reproduction occurs only under a limited range of environmental conditions. In order to model this effect we used a threshold fecundity function (F_2) (Fig. 1):

$$F_2(\bar{G}) = \frac{F}{1 + a/\sqrt{1 + a^2}} \times \left(\frac{\bar{G} - a}{\sqrt{1 + (\bar{G} - a)^2}} + \frac{a}{\sqrt{1 + a^2}} \right) \tag{13}$$

where a is the threshold of the average gain required to initiate reproduction (Fig. 1).

2.3. The aggregated model

When parameter k is large (see Eq. (3)), two different time scales are involved in the dynamics, a fast one

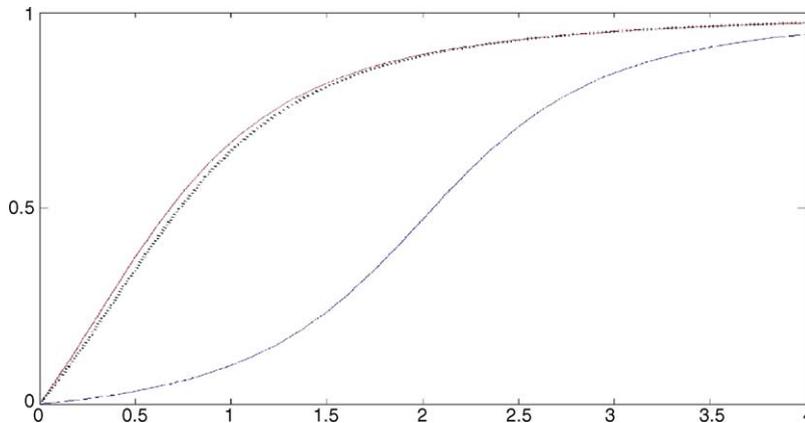


Fig. 1. Threshold fecundity function of average gain. $F = 1$, $a = 0.3$, $a = 0.4$, $a = 2$.

corresponding to the game and a slow one corresponding to the demographic model. In that case, we can apply aggregation methods. The idea is to consider the events occurring at the faster time scale as being instantaneous compared to the slower events. This means that fewer variables (also called macro-variables (Iwasa et al., 1987)) are needed to describe the evolution of the system. To carry out aggregation we built up a reduced system.

If the consistency between the dynamics of the global variables in the original and reduced (or aggregated) system is only approximate, it is referred to as an approximate aggregation (Iwasa et al., 1989). Approximate aggregation has been developed extensively (Auger and Poggiale, 1998; Bravo de la Parra and Sanchez, 1998; Bravo de la Parra et al., 1999; Sanz and Bravo de la Parra, 1999; Auger and Bravo de la Parra, 2000) for systems with two time scales. This kind of aggregation has been used to study both continuous (Auger and Poggiale, 1996; Auger and Pontier, 1998; Bernstein et al., 1999; Pontier et al., 2000; Auger et al., 2000; Lett et al., 2003) and discrete (Charles et al., 1998, 2000) models in ecology.

In our case, the complete model is a three dimensional model as follows:

$$N(t + 1) = \mathbf{LJ}^k N(t) \tag{14}$$

In the first step, we look for the fast equilibrium of the system. Two cases occur:

- (i) assuming that $G < C$, there is a mixed stable fast equilibrium:

$$n_H^* = \left(\frac{G}{C}\right) n_2 \quad \text{and} \quad n_D^* = \left(1 - \frac{G}{C}\right) n_2 \tag{15}$$

When replacing the variables $n_H(t)$ and $n_D(t)$ of the complete model by those of the fast equilibrium, the average costs and gains become:

$$\bar{C}_D = 0 \quad \text{and} \quad \bar{C}_H = \frac{G}{2} \tag{16}$$

$$\bar{G}_D = \frac{G}{2} \left(1 - \frac{G}{C}\right) \quad \text{and} \quad \bar{G}_H = G \left(1 - \frac{G}{2C}\right) \tag{17}$$

- (ii) assuming that $G > C$, there is a pure hawk stable fast equilibrium:

$$n_H^* = n_2 \quad \text{and} \quad n_D^* = 0 \tag{18}$$

When replacing the variables $n_H(t)$ and $n_D(t)$ of the complete model by those of the fast equilibrium, the average costs and gains are given by the following expressions:

$$\bar{C}_D = 0 \quad \text{and} \quad \bar{C}_H = \frac{C}{2} \tag{19}$$

$$\bar{G}_D = 0 \quad \text{and} \quad \bar{G}_H = \frac{G}{2} \tag{20}$$

It must be noted that there is continuity, i.e. average gains and costs in mixed and pure hawk cases become equal at the separation line between the two models, when $G = C$.

In the next step, in the two cases (mixed and pure hawk population), we included average costs and gains calculated at the fast equilibrium into the survival and fecundity functions. Lastly, a simple calculation allows us to obtain the aggregated model:

$$\tilde{N}(t + 1) = \tilde{L}\tilde{N}(t) \tag{21}$$

where $\tilde{N}(t) = (n_1(t), n_2(t))^T$ and where the aggregated Leslie matrix reads:

$$\tilde{L} = \begin{pmatrix} 0 & \tilde{F} \\ S_1 & \tilde{S} \end{pmatrix}, \tag{22}$$

Where the global parameters \tilde{S} and \tilde{F} of the mixed case are given by:

$$\begin{aligned} \tilde{S} &= \left(\frac{G}{C}\right) S_H + \left(1 - \frac{G}{C}\right) S_D \quad \text{and} \\ \tilde{F} &= \left(\frac{G}{C}\right) F_H + \left(1 - \frac{G}{C}\right) F_D, \end{aligned} \tag{23}$$

And where the global parameters \tilde{S} and \tilde{F} of the pure hawk case are given by:

$$\tilde{S} = S_H \quad \text{and} \quad \tilde{F} = F_H, \tag{24}$$

where hawk (dove) survival and fecundity depend on average costs (gains) as explained above. This aggregated matrix is irreducible and primitive and therefore has a unique dominant eigenvalue which corresponds to the asymptotic growth rate of the total population (Caswell, 2001). The aggregated matrix has two real

eigenvalues, one positive and one negative. The dominant positive eigenvalue is given by Eq. (25):

$$\bar{\lambda} = \frac{\tilde{S} + \sqrt{\tilde{S}^2 + 4\tilde{F}S_1}}{2} \quad (25)$$

In which global parameters \tilde{F} and \tilde{S} are given in terms of hawk and dove fecundity and survival through expressions (23) and (24).

3. Results

In our model, G represents an environmental gradient, from poor to rich environments and C represents an escalating gradient, from non-aggressive to aggressive species. G can represent the quality of the environment, from favourable (low G value) to unfavourable (high G value). C can be considered as the ability for an adult to provoke weak injuries (small C value) or strong injuries (large C value) during an escalated contest. In our model, injuries provoke an extra mortality and reduce adult survival. For example, we can think about species with more or less long antlers which allow them causing more or less injuries during an escalated contest.

Our main results show the asymptotic growth rate of the total population $\bar{\lambda}$ with respect to gain G and cost C . We show the graph of function, $\bar{\lambda} = f(G, C)$ for the Holling and threshold fecundity functions. When G and C are given, we consider a particular species in a given environment and the model calculates the growth rate of the population.

Now, if we consider the evolutionary time scale, the structure of the population is expected to change slowly. Hawk and dove tactics might be associated to genotypes (Akin, 1979; Crow and Kimura, 1970; Kimura, 1958). For example, in cats (Pontier et al., 1995), an allele is correlated to the aggressiveness. Under this hypothesis, we can think that the individuals could evolve with different cost values. For example, deer species have developed some extravagant characteristics like their antlers. In other species, parts of body can become some weapons useful during contests (MacFarland, 1999).

In our model, we already considered the behavioural time scale (game dynamics) and the population time scale (Leslie dynamics). Now, we shall take into

account a third time scale, the evolutionary time scale (slower than the population one). At the evolutionary time scale, mutations can occur which can generate new individuals with different C values. At this time scale, mutations occur (through a process which is not modelled here) and allow exploring a small C -domain around C , either $C+dC$ or $C-dC$. Individuals with different C values compete and we assume that the population having the largest growth rate $\bar{\lambda}$ is going to invade.

Similarly, we assume that individuals can disperse in space and explore different environments. At the evolutionary time scale, we assume that population survives in the more favourable environment corresponding to the maximum growth rate $\bar{\lambda}$ with respect to G .

In other words, at the evolutionary time scale, mutation and selection leads to a slow displacement on the surface $\bar{\lambda} = f(G, C)$ in the direction of the positive gradient towards the local maximum of the growth rate $\bar{\lambda}$ with respect to G and C values.

3.1. Holling fecundity function

We have computed numerically the asymptotic growth rate $\bar{\lambda}$ of the aggregated matrix \bar{L} which is presented as a function of gain G and cost C in Fig. 2(a) where some parameters are chosen so to correspond to the fallow deer (*Dama dama*) case as follows, $F=1$, $S=0.85$, $S_1=0.65$ (Pélabon, 1994; Putman, 1985), and the others are chosen as follows $\alpha=0.4$, $\gamma=0.5$.

First, it must be noted that when $\bar{\lambda} < 1$, the population goes to extinction and when $\bar{\lambda} > 1$, the population is viable and can grow. Fig. 2(b) shows that there are two domains of viability.

- A larger domain in the case of a mixed population ($G < C$). For each C -value, the curve has a maximum with respect to G . Therefore, for each population with a given C -value, there exists a most favourable environment. The line of maxima of this domain of viability is almost parallel to the C -axis. Therefore, this line of maxima corresponds to a population living in a rather unfavourable environment. The dove proportion decreases when the cost increases. Individuals of species which have developed dangerous weapons which can cause strong injuries during an escalated contest should thus be less aggressive.

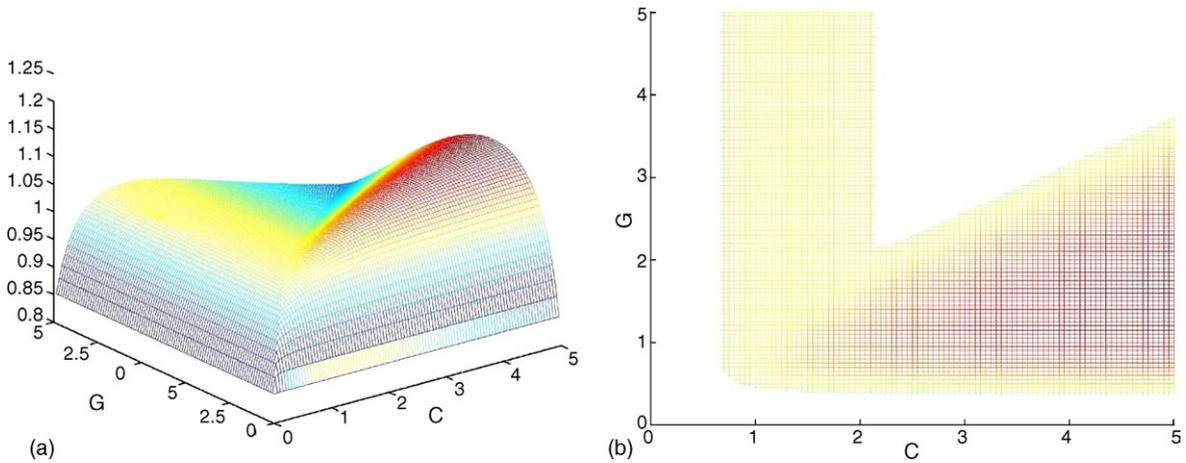


Fig. 2. Holling fecundity function. $F=1, S=0.85, S_1=0.65, \alpha=0.4, \gamma=0.5$. (a) Asymptotic rate of growth of the population as a function of gain (G) and cost (C). (b) Viability domains $\bar{\lambda} > 1$.

- A smaller domain in the case of a pure hawk population ($G > C$). For each G -value, the curve has a maximum which is almost at a constant and small C -value. This corresponds to populations in which individuals cannot cause high costs during an escalated contest but which are pure hawk. During any encounter, individuals always escalate but do not cause strong injuries. This case can occur in any kind of environment.

A global maximum (for a limited range of positive G and C) is found for a mixed population mainly dove in a rather unfavourable environment.

Fig. 3(a) shows the asymptotic growth rate $\bar{\lambda}$ of the aggregated matrix \bar{L} where all parameters are similar as in Fig. 2, except $\alpha = 1$. Fig. 3(b) shows that now there is only one domain of viability in the case of a mixed population. An increase of the parameter α provokes a decrease of the survival of one-year-old individuals.

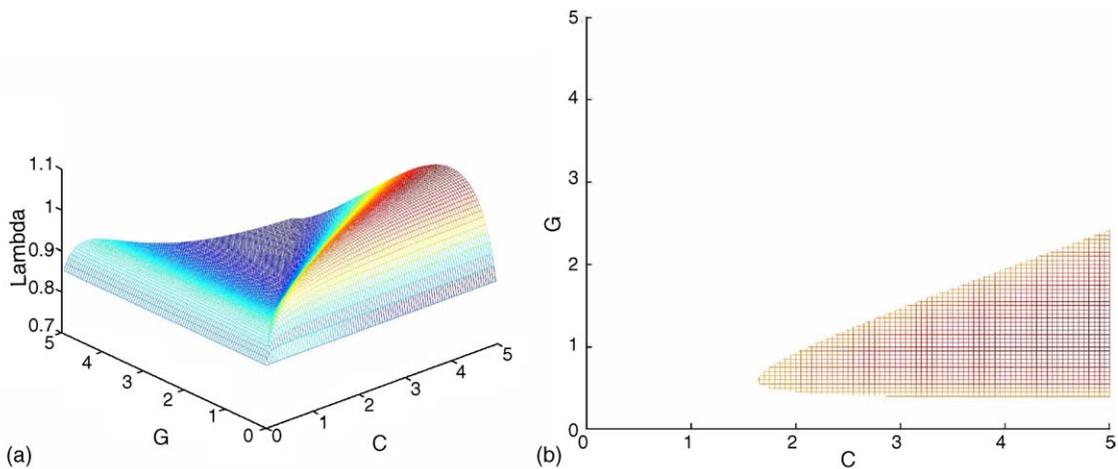


Fig. 3. Holling fecundity function. $F=1, S=0.85, S_1=0.65, \alpha=1, \gamma=0.5$. (a) Asymptotic rate of growth of the population as a function of gain (G) and cost (C). (b) Viability domains $\bar{\lambda} > 1$.

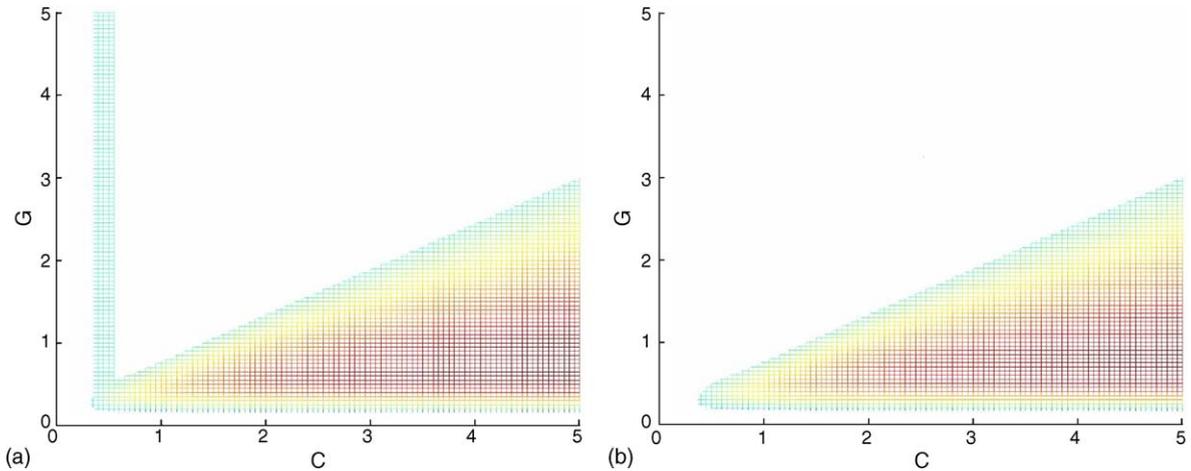


Fig. 4. Threshold fecundity function. Viability domains $\bar{\lambda} > 1$. $F = 1$, $S = 0.85$, $S_1 = 0.65$, $\alpha = 1$. (a) $a = 0.3$; (b) $a = 0.4$.

Thus, the asymptotic growth rate decreases and the domain of viability of the hawk population can even disappear.

3.2. Fecundity function with a threshold effect

Fig. 4(a) shows the domain of viability as a function of G and C , where the parameters are similar to the case of Fig. 2, $F = 1$, $S = 0.85$, $S_1 = 0.65$, $\alpha = 0.4$, but with parameter a of the threshold fecundity function: $a = 0.3$. This figure shows the same result as Fig. 2(b) with two viability domains with the same interpretation as before. Fig. 4(b) shows the viability domain for a small increase of parameter a ($a = 0.4$). This figure shows that a small increase of the threshold a can provoke the disappearance of the pure hawk viability area. For any a larger than 0.4, there is a single viability domain for a mixed population which is smaller when a increases.

4. Discussion and conclusion

The two previous models show that behavioural interactions between individuals can have important effects on the population growth rate. In these models, we have tried to incorporate simple knowledge about behavioural plasticity of individuals according to the level of aggressiveness to get access to a critical resource. Such behavioural plasticity is widespread among vertebrate population in which individuals dis-

play different behaviour according to their body size, age and experience (Lott, 1991).

To summary, in both cases (Holling and threshold fecundity functions) our results show that the asymptotic growth rate function, $\bar{\lambda} = f(G, C)$, has two domains of viability. Therefore, two scenarios occur: all individuals of the population display a mixed tactic with rather small gain or are all hawks at low cost. When the gain is low or medium, it seems better to mainly avoid contests and thereby costs for a low reward. On the other hand, it seems better to fight when the reward is high but at low cost. In this case, we can find a population composed of hawks only but with low costs, i.e. leading to few injuries during an escalated contest.

Our model is based on the coupling between population dynamics and game dynamics. This coupling allowed us to describe the overall population dynamics, with individuals using different tactics during their life and to analyse the effects of different behavioural changes on population growth according to biological processes going on at different time scales (day for contests, year for the demography). However, a realistic model would integrate other tactics (such as retaliator and bully). It would also be useful to take into account non-linear processes, such as density-dependent survival of juveniles (Gaillard et al., 2000).

Aggregation methods have been applied to the study of dynamical systems with two time scales (Auger and Poggiale, 1996; Bravo de la Parra et al., 1999; Iwasa et al., 1989; Sanchez et al., 1995). In our model, the

game process is repeated several times within a generation, whereas the demographic process is applied only once, so that the game operates on a fast-time scale and the demography on a slow-time scale. Assuming that the fast process goes to a stable equilibrium, the aggregated model can be used to evaluate the consequences of changing the proportion of hawks and to study the consequences of changing in individual behaviour on population growth rate. However, aggregation methods could be more useful in the context of a non-linear population model because in this case the reduced (aggregated model) could at least in some cases be more tractable than the complete model.

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