

A density-dependent model describing age-structured population dynamics using hawk–dove tactics

M. Marvá^{a*}, A. Moussaoui^b, R. Bravo de la Parra^a and P. Auger^{c,d}

^aDepartamento de Matemáticas, Universidad de Alcalá, 28871 Madrid, Spain; ^bDepartment of Mathematics, Faculty of Sciences, University of Tlemcen, Tlemcen, Algeria; ^cUR UMMISCO, IRD France Nord, F-93143 Bondy, France; ^dUPMC Univ Paris 06, UMI 209, UMMISCO, F-75005 Paris, France

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In this paper we deal with a nonlinear two-timescale discrete population model that couples age-structured demography with individual competition for resources. Individuals are divided into juvenile and adult classes, and demography is described by means of a density-dependent Leslie matrix. Adults compete to access resources; every time two adults meet, they choose either being aggressive (hawk) or non-aggressive (dove) to get the best pay-off. Individual encounters occur much more frequently than demographic events, what yields that the model takes the form of a two-timescale system. Approximate aggregation methods allow us to reduce the system while preserving at the same time crucial asymptotic information for the whole population. In this way, we are able to describe the total population size as function of individual aggressiveness level and environmental richness. Model analysis shows a general trend with species that look for richer environment having smaller proportions of hawk individuals with larger costs.

Keywords: game dynamics; Leslie model; aggregation methods; individual behaviour; aggressiveness

1. Introduction

An important goal of population dynamics is taking into account the behavioural tactics that individuals may adopt to increase their population fitness [11]. In this frame we consider a population structured by age, with juvenile and adult classes, and by behavioural tactics, adults choose between classical hawk and dove tactics in order to get access to a resource.

The principal goal of this paper is analysing the strategies that maximize population fitness. Concerning strategies, we suppose, on the one hand, that adult individuals could adopt an aggressive tactics in order to hoard resources with the drawback of larger costs due to injuries and extra mortality and, on the other hand, they might alternatively use a non-aggressive tactics that entails sharing resources without fight costs. We describe the population dynamics by means of a simple model susceptible of being studied analytically that, at the same time, allows revealing the general trends of our main goal.

The mathematical model takes the form of a discrete system that couples two processes: the adult competition for resources, described by the classical hawk–dove game model [11,14,17,23], and the demography depicted by a density-dependent Leslie-like

*Corresponding author. Email: marcos.marva@uah.es

model [10] whose matrix entries depend on the densities of juvenile, hawk adult and dove adult individuals. We also assume that game dynamics, produced at adult encounters, acts at a faster timescale than population demography. It is the existence of these two different timescales which allows using approximate aggregation methods [4,5] to reduce the dimension of the complete initial model obtaining a mathematically tractable aggregated model whose state variables are the juvenile and adult densities.

Though there are several works coupling fast game and slow population/community dynamics at continuous time, using two-timescale ordinary differential equation systems [2,3,13,16], to our knowledge, few works have been devoted to the same setting at discrete time. We could mention a previous study [8] where such kind of model was presented. In contrast to that study we present a fully nonlinear model (the model in [8] was linear) by considering the more realistic case of density-dependent recruitment of juveniles to adult stage and adult fertility and survival rates depending on hawks/doves densities and on fighting costs and gains. We also include in this study an explicit formulation of the hawk–dove discrete model (which is obviated in [8]) and prove that aggregation results apply.

This paper is organized as follows. In Section 2, we first present the two sub-models, the game dynamics and the Leslie models, which are subsequently coupled to obtain the complete model. Section 3 is devoted to the analysis of the complete model through the aggregated model. Section 4 includes the presentation of results and perspectives. Finally, Appendix containing technical results conclude the paper.

2. Presentation of the model

We consider an age-structured population with two age classes: non-reproductive (juvenile) and reproductive (adult) individuals. Reproductive individuals are assumed to compete to access the available resources and, according to their behaviour, belong to one of the following categories: aggressive or non-aggressive. We denote $n_1(t)$, $n_H(t)$ and $n_D(t)$, respectively, the densities of juveniles, hawk adults and dove adults. The population vector at time t is thus: $N(t) = (n_1(t), n_H(t), n_D(t))^T \in \Omega_3$ where $\Omega_3 := \{(n_1, n_H, n_D) \in \mathbb{R}^3; n_i \geq 0, i = 1, H, D\}$ and T denotes the transposition. We also note the total number of adult individuals at time t by $n_2(t) = n_H(t) + n_D(t)$.

2.1 Fast process: game dynamics

We assume that reproductive individuals frequently encounter each other and compete for resources, food or mates. The two behavioural phenotypes, hawk and dove, are assumed to be achievable by any adult, whatever their genotype is. Individuals may choose these alternative tactics according to the conspecifics they encounter (due to physical strength, dominance rank of the opponent, etc.). Each encounter event leads to a pay-off, depending on the tactics adopted by the two opponents. One may assume that, after a sufficiently large number of encounters, each individual is able to estimate the success of each tactics and will more often play the tactics that corresponds, in average, to the best pay-off. We assume that the proportion of individuals playing a strategy H or D increases (decreases) when the difference between the pay-off of this tactics and the average pay-off in the population is positive (negative). These hypotheses are included in the model through the classical hawk–dove pay-off matrix, denoted A , whose coefficients $a_{i,j}$ represent the pay-offs of individuals playing the i

strategy against a j strategist. Matrix A reads as follows:

$$A = \begin{pmatrix} \frac{G-C}{2} & G \\ 0 & \frac{G}{2} \end{pmatrix},$$

where G is the gain and C is the cost of injuries resulting of fights. Both G and C are positive.

The discrete time hawk–dove game equations (see equation (16.4) in [10]) can be deduced by an appropriate discretization of the corresponding ordinary differential equation system. In Ahmed and Hegazi [1], these discrete equations are studied. Using them we define the fast dynamics for adults through the following map:

$$P_2(n_H, n_D) := \begin{pmatrix} \frac{-(G+C)n_H^2 n_2 + (2G+C)n_H n_D^2}{-Cn_H^2 + (G+C)n_2^2} \\ \frac{Gn_D^2 n_2 + Cn_D n_2^2}{-Cn_H^2 + (G+C)n_2^2} \end{pmatrix} \quad (1)$$

if $n_2 \neq 0$, where we recall that $n_2 = n_H + n_D$ and $P_2(0, 0) = (0, 0)$. As the juveniles are not affected by fast dynamics the map representing it for the whole population is

$$P(n_1, n_H, n_D) = (n_1, P_2(n_H, n_D)), \quad (2)$$

where $P: \Omega_3 \rightarrow \Omega_3$ and P_2 is the map defined in (1).

2.2 Slow dynamics: demography

Demography is driven by a density-dependent Leslie matrix of the form

$$L(n_1, n_H, n_D) = \begin{pmatrix} 0 & F_H(n_H, n_D) & F_D(n_H, n_D) \\ qS_1(n_1) & S_H(n_H, n_D) & 0 \\ (1-q)S_1(n_1) & 0 & S_D(n_H, n_D) \end{pmatrix}, \quad (3)$$

where $S_1(n_1)$ is the juvenile's survival rate and parameter $q \in (0, 1)$ represents the proportion of juveniles becoming hawk adult; $S_i(n_H, n_D)$, with $i = H, D$, are the hawk and dove survival rates and $F_i(n_H, n_D)$ the corresponding fecundity rates.

Juvenile survival rate $S_1(n_1)$ is assumed density dependent and following [6] we define it as

$$S_1(n_1) = \frac{S_1}{1 + \beta n_1},$$

where S_1 and β are strictly positive constants. This function is monotone decreasing, i.e. the survival rate of juveniles decreases as juvenile density increases.

Concerning adult survival rates, we assume that escalated contests cause injuries which provoke a decrease in adult survival according to

$$S_i(n_H, n_D) = S_i e^{-\alpha \bar{C}_i(n_H, n_D)} \quad i = H, D,$$

where S_i , for $i = H, D$, is a positive constant, $\bar{C}_i(n_H, n_D)$ is the average cost received by an individual of subgroup i and $\alpha > 0$ is a constant regulating the effect of the average cost on

the survival rate. $\bar{C}_i(n_H, n_D)$ is calculated by adding the cost for hawks and doves weighted by the current proportion of hawks and doves. So, the average dove cost is zero as doves do not fight and so they do not get injured:

$$\bar{C}_D(n_H, n_D) = 0 \frac{n_H}{n_2} + 0 \frac{n_D}{n_2} = 0.$$

On the other hand, when a hawk encounters another hawk they share cost, while there is no cost for a hawk meeting a dove, which yields the average hawk cost:

$$\bar{C}_H(n_H, n_D) = \frac{C n_H}{2 n_2} + 0 \frac{n_D}{n_2}.$$

Finally, we assume that fecundity rates $F_i(n_H, n_D)$ depend on the average gains $\bar{G}_i(n_H, n_D)$, for $i = H, D$, which are calculated as done for the average costs. Doves share gains when meet each other but they get no gain when encounter a hawk, so that

$$\bar{G}_D(n_H, n_D) = 0 \frac{n_H}{n_2} + \frac{G n_D}{2 n_2}.$$

Hawks share gains when meeting another hawk and they get full gain when encountering a dove, thus

$$\bar{G}_H(n_H, n_D) = \frac{G n_H}{2 n_2} + G \frac{n_D}{n_2}.$$

For the precise form of the fecundity rates we consider two different cases.

The first case is appropriate for species for which the amount of resource has a continuous effect on fecundity, we propose for them Holling-type fecundity rates:

$$F_i(n_H, n_D) = \frac{F_i \bar{G}_i(n_H, n_D)}{\gamma + \bar{G}_i(n_H, n_D)} \tag{4}$$

for $i = H, D$, where F_i and γ are positive constants, being γ the parameter that permits to control the ‘speed’ to reach the plateau of fecundity.

The second case corresponds to species where individual must accumulate a given amount of resource before reproduction is available. This effect is modelled using threshold fecundity rates:

$$F_i(n_H, n_D) = \frac{F_i}{1 + a/\sqrt{1 + a^2}} \times \left(\frac{\bar{G}_i(n_H, n_D) - a}{\sqrt{1 + (\bar{G}_i(n_H, n_D) - a)^2}} + \frac{a}{\sqrt{1 + a^2}} \right), \tag{5}$$

for $i = H, D$, where F_i and a are positive constants, being a the threshold of the average gain required for initial reproduction [8].

We point out that the precise form of these functions is not crucial in the carried out analytical study of the model. They will only be explicitly considered in the numerical simulations.

2.3 The complete model

We build up the complete model combining these two processes presented in Sections 2.1 and 2.2. Compared to the demographic process, individual encounters and fights for resources are much more frequent, so that we consider them acting at different timescales. We denote k a positive integer measuring the timescales ratio assuming that, on average, k adult encounters take place within each reproductive period. We express the discrete system using the time unit associated with reproduction; thus, we let game dynamics acts k times, $P^{(k)}(\cdot)$, followed by the demographic dynamics, represented by matrix L , getting the following system:

$$N_k(t+1) = L(P^{(k)}(N_k(t))) \cdot P^{(k)}(N_k(t)), \quad (6)$$

where we call $N_k(t)$ the vector of state variables at time t .

3. Analysis of the model

In this section we accomplish the analysis of the complete model (6) using approximate aggregation techniques, in particular, following those results in Sanz et al. [14]. Let us briefly describe the approximate aggregation procedure. This approach assumes that fast dynamics instantaneously achieves an equilibrium, that is, there exists

$$\lim_{k \rightarrow \infty} P^{(k)}(N) = \bar{P}(N), \quad \text{for every } N \in \Omega_3. \quad (7)$$

Replacing in the complete system (6) the fast dynamics by its equilibrium (7), we get the so-called *auxiliary* system

$$N(t+1) = L(\bar{P}(N(t))) \cdot \bar{P}(N(t)) \quad (8)$$

which approaches the complete model for k large enough (note that parameter k is not needed anymore). It is also assumed that \bar{P} admits a suitable decomposition

$$\bar{P} = E \circ G, \quad (9)$$

with $G: \Omega_3 \rightarrow \Omega_2$ and $E: \Omega_2 \rightarrow \Omega_3$, where $\Omega_2 \subset \mathbb{R}^2$ is the non-negative cone. Then, defining the so-called *global variables* $Y = G(N)$ it is obtained a reduced (also called aggregated) system for them:

$$Y(t+1) = G(L(E(Y(t)))) \cdot E(Y(t)). \quad (10)$$

Next we build up the aggregated system associated with system (6).

3.1 Reduction in the model

First of all, we need to calculate the limit in (7). This is done in the next proposition where we find, as in the classical hawk–dove game, that if cost, C , is larger than gain, G , the adult population tends to have hawks in proportion G/C and doves in proportion $1 - G/C$, while in the opposite case all adults become hawks.

PROPOSITION 3.1. Let P be the map defined in (2). Then, for each $N = (n_1, n_H, n_D) \in \Omega_3$ we have that

$$\bar{P}(N) = \lim_{k \rightarrow \infty} P^{(k)}(N) = (n_1, \nu_H^* n_2, (1 - \nu_H^*) n_2)^T \tag{11}$$

where $\nu_H^* = G/C$ if $G < C$ and $\nu_H^* = 1$ if $G > C$.

Proof. See Appendix. □

$\bar{P}(N)$ can be expressed in terms of a 3×2 -matrix, \bar{P}^* , and the vector of total densities of juveniles and adults $(n_1, n_2)^T$ as $\bar{P}(N) = \bar{P}^* \cdot (n_1, n_2)^T$ where

$$\bar{P}^* = \begin{pmatrix} 1 & 0 \\ 0 & \nu_H^* \\ 0 & 1 - \nu_H^* \end{pmatrix}.$$

Now, it is straightforward that the decomposition in (9), $\bar{P}(N) = E \circ G(N)$, can be done taking

$$G(n_1, n_H, n_D) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} \cdot N := B \cdot N = \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}$$

and

$$E(n_1, n_2) = \bar{P}^* \cdot \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}.$$

So, the global variables $G(N)$ are the total densities of juveniles and adults and we can calculate the aforementioned aggregated system (10):

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix} = B \cdot L \left(\bar{P}^* \cdot \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix} \right) \cdot \bar{P}^* \cdot \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}$$

which simplifies to

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \bar{F} \\ \frac{S_1}{1+\beta n_1(t)} & \bar{S} \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}, \tag{12}$$

where

$$\bar{F} = \nu_H^* F_H(\nu_H^* n_2, (1 - \nu_H^*) n_2) + (1 - \nu_H^*) F_D(\nu_H^* n_2, (1 - \nu_H^*) n_2)$$

and

$$\bar{S} = \nu_H^* S_H(\nu_H^* n_2, (1 - \nu_H^*) n_2) + (1 - \nu_H^*) S_D(\nu_H^* n_2, (1 - \nu_H^*) n_2),$$

where ν_H^* is defined as before. We point out that both \bar{F} and \bar{S} are constant because F_i and S_i , with $i = H, D$, depend on the proportions of hawks and doves, reflected in ν_H^* , and not on the adult total density n_2 (see Section 2.2).

3.2 Analysis of the model

We first discuss the asymptotic behaviour of the aggregated system (12) in Proposition 3.2. Then, we use the main theorem in Sanz et al. [14] to obtain some results on the asymptotic behaviour of the complete system (6) which are included in Theorem 3.1.

PROPOSITION 3.2. For system (12):

1. If

$$\bar{F}S_1 + \bar{S} < 1, \quad (13)$$

the trivial equilibrium is globally asymptotically stable.

2. If

$$\bar{F}S_1 + \bar{S} > 1, \quad (14)$$

system (12) possesses an unique positive equilibrium:

$$n^* = (n_1^*, n_2^*) = \left(\frac{\bar{F}S_1 + \bar{S} - 1}{\beta(1 - \bar{S})}, \frac{n_1^*}{\bar{F}} \right) \quad (15)$$

which is asymptotically stable.

Proof. (0,0) is an equilibrium of system (12). Any solution $(n_1(t), n_2(t))$ of system (12) is bounded from above by the solution $Z(t) = (z_1(t), z_2(t))$ for the same initial conditions of system

$$Z(t+1) = \begin{pmatrix} 0 & \bar{F} \\ S_1 & \bar{S} \end{pmatrix} Z(t). \quad (16)$$

Condition (13) implies that (0, 0) is a globally asymptotically stable for the linear system (16) what yields 1.

A necessary condition for system (12) to have a non-trivial equilibrium $n^* = (n_1^*, n_2^*)$ is that matrix

$$\begin{pmatrix} 0 & \bar{F} \\ \frac{S_1}{1+\beta n_1(t)} & \bar{S} \end{pmatrix}$$

has an eigenvalue equal to 1, that is, $1 - \bar{S} - \bar{F}S_1/(1 + \beta n_1) = 0$. Solving this equation for n_1 we obtain

$$n_1^* = \frac{\bar{F}S_1 + \bar{S} - 1}{\beta(1 - \bar{S})}$$

which is positive if and only if condition (14) holds.

To study the stability of n^* , we apply the Jury's test ([13]) to the matrix of the linearization of system (12) at n^* . Calling M the map associated with (12), the aforementioned matrix is the Jacobian at n^* , $JM(n^*)$, and the conditions for asymptotic

stability are $|\text{tr}(JM(n^*))| < 1 + \det(JM(n^*)) < 2$, that is,

$$\bar{S} < 1 - \frac{(1 - \bar{S})^2}{S_1 \bar{F}} < 2.$$

The rightmost inequality obviously holds and the leftmost inequality is straightforwardly deduced from inequality (14). □

The asymptotic results obtained in Proposition 3.2 are now extended to the complete system (6). Roughly speaking, we prove that, for sufficiently large timescales ratio, all solutions of (6) tend to zero when condition (13) holds, while in the case that condition (14) is met (6) possesses an asymptotically stable positive equilibrium which can be approximated together with its basin of attraction in terms of n^* and its own basin of attraction.

THEOREM 3.1. *Let us consider the complete system (6)*

$$N_k(t + 1) = L(P^{(k)}(N_k(t))) \cdot P^{(k)}(N_k(t)).$$

Then:

1. *If condition (13), $\bar{F}S_1 + \bar{S} < 1$, holds then there exists an integer $k_1 > 0$ such that for each $k \geq k_1$ the trivial equilibrium is globally asymptotically stable.*
2. *If condition (14), $\bar{F}S_1 + \bar{S} > 1$, holds then there exists $r > 0$ and an integer $k_0 > 0$ such that:*
 - a. *For each $k \geq k_0$ there exists a unique positive asymptotically stable equilibrium N_k^* , verifying $\|N_k^* - E(n_1^*, n_2^*)\| < r$ and*

$$\begin{aligned} \lim_{k \rightarrow \infty} N_k^* &= E(n_1^*, n_2^*) \\ &= \left(\frac{\bar{F}S_1 + \bar{S} - 1}{\beta(1 - \bar{S})}, v_H^* \frac{\bar{F}S_1 + \bar{S} - 1}{\bar{F}\beta(1 - \bar{S})}, (1 - v_H^*) \frac{\bar{F}S_1 + \bar{S} - 1}{\bar{F}\beta(1 - \bar{S})} \right) \end{aligned}$$

- b. *If $N_0 = (n_1^0, n_H^0, n_D^0) \in \Omega_3$ is such that $n_0 = G(N_0) = (n_1^0, n_H^0 + n_D^0)$ is in the basin of attraction of n^* in system (12) then N_0 is in the basin of attraction of N_k^* in system (6).*

Proof. See Appendix. □

4. Discussion

Our results are represented in a synthetic manner in Figures 1 and 2 displaying the total population density at the equilibrium when a Holling fecundity function (left) or a thresholds fecundity function (right) is considered. We point out that the outcome of the model for both fecundity functions is qualitatively the same. In fact, the quantitative differences are not significant so that both figures admit a common description. The total population density can be understood as a measure of the population fitness with respect to game parameters that relate to individual behaviour, the gain G and the cost C . Namely, we consider here that populations having the largest total density at equilibrium might have a better chance to survive in the long term. Therefore, we assume that individuals would try to find an environment that maximizes the total population density in the long term.

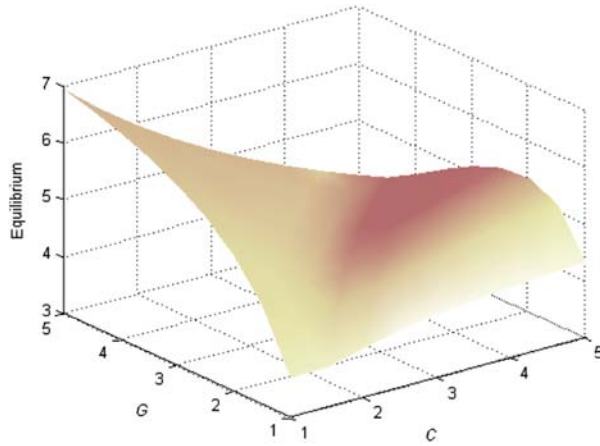


Figure 1. Equilibrium n^* as a function of gain (G) and cost (C) considering Holling-type fecundity function (4). Parameter values $S_1 = 0.7$, $\beta = 1$, $\gamma = 0.8$, $F = 1$ and $\alpha = 0.05$.

In our model G , the gain of the game can be seen as the resource biomass that is obtained when an individual is the winner of a contest. Therefore, a gradient of gain G can be considered as a gradient of resource abundance from poor (associated with small gains) to rich (associated with large gains) environments. A gradient of cost can be considered as a measure of individual aggressiveness, from few aggressive individuals or species (associated with small costs) to very aggressive specimens (associated with large costs).

Each plotting displayed in Figures 1 and 2 is composed of two parts that should be considered separately below and above the bisectrix $G = C$. Indeed, when $G > C$, the adult population is pure hawk while in the domain $G < C$, the population is mixed with a constant proportion of hawks at the fast equilibrium G/C . In the first domain, $G > C$, the total population fitness is a monotone increasing function of G at fixed cost. This signifies that the population fitness always increases when the environment is richer and this makes sense. On the contrary, at fixed gain G , the population fitness increases for smaller costs.

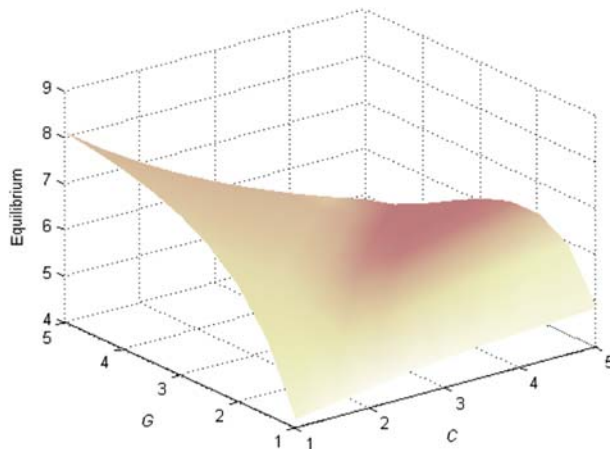


Figure 2. Equilibrium n^* as a function of gain (G) and cost (C) considering threshold fecundity function (5). Parameter values $S_1 = 0.7$, $\beta = 1$, $\gamma = 0.8$, $F = 1$, $\alpha = 0.05$ and $a = 0.1$.

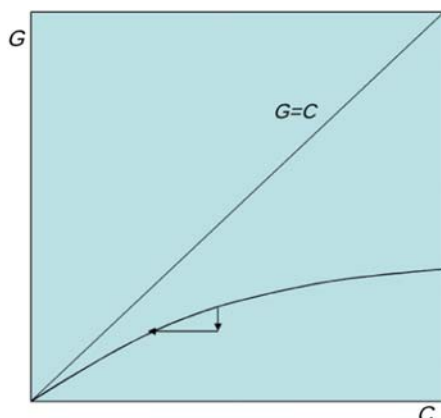


Figure 3. Hill curve of local maxima and the effect of global change and human activities on the population size. As G decreases, the population size leaves the top of the hill. Reducing aggressiveness, C , will let the population reach the maximum fitness at the top of the hill.

Therefore, in a pure hawk population, as expected, the total fitness increases when the adults are less aggressive leading to less injuries and to smaller mortality. In the second domain, $G < C$, the population is mixed with hawks and doves. In that domain, if one keeps constant the cost C , we observe a maximum of the population fitness when the gain increases from zero. Therefore, the model predicts that according to the level of aggressiveness of the population, there is a particular type of environment that maximizes the population fitness. Similarly, if one keeps the gain G constant, there is a cost that maximizes the population fitness. In other words, in a given environment, there is a level of aggressiveness in the population that maximizes the population fitness. Moreover, Figures 1 and 2 show a curve of local maxima associated with a hill line observed in the domain $G < C$. It is important to note that the population fitness along this hill increases for larger gains and costs. Therefore, it signifies that populations might increase their fitness by choosing to settle in a better environment (larger G) as well as by adopting a more aggressive behaviour (larger C). However, the hill curve has a slope that slightly decreases when C increases. Therefore, the population fitness is increased for populations in which the proportion of aggressive individuals decreases when the cost becomes larger. In other words, the model predicts that when the cost is high, the proportion of aggressive individuals should be smaller in order to maximize the population fitness. Behavioural strategies maximizing population fitness range from populations with rather large proportions of aggressive individuals at small cost to populations with a very small proportion of aggressive individuals at much larger cost. Consequently, the model shows a general trend with species looking for richer environment (bigger G) having small proportions of hawk individuals at large cost, i.e. individuals rarely fighting but with strong injuries when fighting occurs.

Global change has an important impact on the environment. As a consequence it makes sense to assume that climate change may progressively modify the quality of the environment. A typical case is that of an environment having abundant rainfalls that, due to global change, might evolve towards a much dryer climate with fewer resources. Similarly, human activities such as industries and settlements have important consequences on ecosystems by reducing habitats quality and access to resources for many animal species. In our model this can be interpreted through parameter G that

decreases together with the quality of the environment. A first response of a population to this decrease could be migrating to other regions where G is larger in order to increase its fitness. However, if we assume that these changes occur in an ecological island then animals must necessarily stay and, in this rather extended case, our model can be used to make predictions about the expected changes in individual behaviour as response to habitat deterioration. Let us analyse the case of a population established in an environment with the maximum fitness associated with the corresponding G -value and suppose that $G < C$, i.e. at a position along the hill curve mentioned in the previous paragraph. The population would be mixed with a constant, G/C , proportion of hawks. Now, we introduce a progressive environment change that implies parameter G to slowly decrease year after year. In that case, the equilibrium point does not remain on the hill curve but will move along the line $C = \text{constant}$ in the direction of smaller G values, see Figure 3. At the same time individuals might also progressively modify their behaviour in response to this evolution and so we can assume that population fitness would tend to slowly return to the hill curve. That means that a plausible response to a slow decrease in G is a progressive individual behaviour change, which could be described by the level of aggressiveness in the population, which is represented by parameter C in our model. Would C increase or decrease? An increase in C would lead to a smaller fitness and therefore would not be selected in the long term. On the contrary, a decrease in C would allow to return to a fitness along the hill curve. Therefore, we can expect in an environment becoming poorer that animals tend to be less aggressive (smaller C) in order to maximize population fitness. Obviously, any change in increasing parameter G , i.e. enriching natural ecosystem, such as protection rules like creation of natural parks, would lead to the opposite result, i.e. an increase in parameter C .

The simple model presented in this work introduces elements enough to show a general trend about effects of individual behaviour on population fitness. Nevertheless, it would be also interesting to consider more realistic models which include different types of dominance associated with different adult sizes or age classes. The existence of different dominance classes could be a useful strategy of some species to avoid too many fightings between individuals as they would only fight against individuals belonging to their own class and not with those of other classes, limiting in this way injuries and global mortality. We intend to treat that issue through a more complex model in future work.

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Appendix

Proof of Proposition 3.1. Let us define $v_H = n_H/n_2$ if $n_2 > 0$ and 0 if $n_2 = 0$. Then $P(N)$ can be written as

$$P(n_1, n_H, n_D) = P(n_1, n_2 v_H, n_2(1 - v_H)) = (n_1, \phi(v_H)n_2, (1 - \phi(v_H))n_2) \tag{17}$$

where function ϕ is defined as follows:

$$\phi(v_H) = \frac{-(G + C)v_H^2 + (2G + C)v_H}{-Cv_H^2 + G + C}. \tag{18}$$

Now, the fact that n_2 is invariant for P allows to express $P^{(k)}$ in terms of $\phi^{(k)}$:

$$P^{(k)}(N) = (n_1, n_2 \phi^{(k)}(v_H), n_2(1 - \phi^{(k)}(v_H))) \tag{19}$$

Function ϕ is monotone increasing on $[0, 1]$, $\phi(0) = 0$, $\phi(1) = 1$ and for any $v_H \in (0,1)$

$$\lim_{k \rightarrow \infty} \phi^{(k)}(v_H) = v_H^* \quad (G/C \text{ if } G < C, 1 \text{ if } G > C) \tag{20}$$

which implies that

$$\bar{P}(N) = \lim_{k \rightarrow \infty} P^{(k)}(N) = (n_1, v_H^* n_2, (1 - v_H^*) n_2)$$

and Proposition 3.1 is proved. □

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Proof of Theorem 3.1. To apply the main results in Sanz et al. [22] and so get proven Theorem 3.1, we need to justify that $\lim_{k \rightarrow \infty} P^{(k)}(N) = \bar{P}(N)$ uniformly on compact sets and the same happens with the limit of their differentials, i.e. $\lim_{k \rightarrow \infty} DP^{(k)}(N) = D\bar{P}(N)$ uniformly on compact sets.

It is straightforward to prove that the limit in (20) is uniform on compact subsets of $(0, 1)$ and from this and (19) we have that the pointwise limit obtained in (3.1) is in fact uniform on compact sets.

To prove that $\lim_{k \rightarrow \infty} DP^{(k)}(N) = D\bar{P}(N)$ uniformly on compact sets, let us, first of all, express $DP^{(k)}(N)$ in terms of $(\phi^{(k)})'$ and also calculate $D\bar{P}(N)$.

From (19) we get

$$DP^{(k)}(N) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \phi^{(k)}(v_H) + (1 - v_H)(\phi^{(k)})'(v_H) & \phi^{(k)}(v_H) - v_H(\phi^{(k)})'(v_H) \\ 0 & 1 - \phi^{(k)}(v_H) - (1 - v_H)(\phi^{(k)})'(v_H) & 1 - \phi^{(k)}(v_H) + v_H(\phi^{(k)})'(v_H) \end{pmatrix}$$

$$DP^{(k)}(N) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix} + \phi^{(k)}(v_H) \begin{pmatrix} 0 & 0 & 0 \\ 0 & 1 & 1 \\ 0 & -1 & -1 \end{pmatrix}$$

$$+ (\phi^{(k)})'(v_H) \begin{pmatrix} 0 & 0 & 0 \\ 0 & (1 - v_H) & -v_H \\ 0 & -(1 - v_H) & v_H \end{pmatrix}.$$

On the other hand, as $\bar{P}(N) = (n_1, v_H^* n_2, (1 - v_H^*) n_2)$ we get that

$$D\bar{P}(N) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & v_H^* & v_H^* \\ 0 & 1 - v_H^* & 1 - v_H^* \end{pmatrix}.$$

Having in mind that $\lim_{k \rightarrow \infty} P^{(k)}(N) = \bar{P}(N)$ uniformly on compact sets, to prove that also $\lim_{k \rightarrow \infty} DP^{(k)}(N) = D\bar{P}(N)$ uniformly on compact sets we only need to show that the following limit is uniform on compact sets of $(0, 1)$,

$$\lim_{k \rightarrow \infty} (\phi^{(k)})'(v_H) = 0.$$

This is straightforward from the fact that $0 < \phi'(v_H^*) < \alpha < 1$ and so there is neighbourhood $I \subset (0, 1)$ of v_H^* such that for every $v_H \in I$ we also have $0 < \phi'(v_H) < \alpha < 1$. Now, the uniform limit (20) and the chain rule to calculate $(\phi^{(k)})'(v_H)$ complete the proof. \square