



Evolutionarily stable transition rates in a stage-structured model. An application to the analysis of size distributions of badges of social status

Jordi Ripoll ^a, Joan Saldaña ^{a,*}, Juan Carlos Senar ^b

^a Dept. d'Informàtica i Matemàtica Aplicada, Campus de Montilivi, Universitat de Girona, E-17071 Girona, Spain

^b Museu de Ciències Naturals de Barcelona, Pg. Picasso s/n, Parc Ciutadella, E-08003 Barcelona, Spain

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Abstract

This paper deals with the adaptive dynamics associated to a hierarchical non-linear discrete population model with a general transition matrix. In the model, individuals are categorized into n dominance classes, newborns lie in the subordinate class, and it is considered as evolutionary trait a vector η of probabilities of transition among classes. For this trait, we obtain the evolutionary singular strategy and prove its neutral evolutionary stability. Finally, we obtain conditions for the invading potential of such a strategy, which is sufficient for the convergence stability of the latter.

With the help of the previous results, we provide an explanation for the bimodal distribution of badges of status observed in the Siskin (*Carduelis spinus*). In the Siskin, as in several bird species, patches of pigmented plumage signal the dominance status of the bearer to opponents, and central to the discussion on the evolution of status signalling is the understanding of which should be the frequency distribution of badge sizes. Though some simple verbal models predicted a bimodal distribution, up to now most species display normal distributions and bimodality has only been described for the Siskin. In this paper, we give conditions leading to one of these two distributions in terms of the survival, fecundity and aggression rates in each dominance class.

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* Corresponding author. Tel.: +34-972 418 834; fax: +34-972 418 792.

E-mail addresses: jripoll@ima.udg.es (J. Ripoll), jsaldana@ima.udg.es (J. Saldaña), jcsenar@intercom.es (J.C. Senar).

1. Introduction

Rohwer proposed in 1975 [1] that the patches of pigmented plumage displayed by several bird species could be related to dominance signalling. The advantage of the system would be that in communicating the dominance status of the bearers, contestants could resolve a potential fight without resorting to costly violence. The so called ‘status signalling hypothesis’, albeit controversial, has been found to work in several birds species [2].

However, we are still far away from a full understanding of the dynamics of a signalling system as the one proposed above. Great controversy exists in relation to how the system could be evolutionarily stable and several disparate hypotheses have been proposed [2–5]. It is still unclear how badges of dominance status should be related to sexual selection processes [2]; although some authors propose that many sexual ornaments have first evolved as armaments in intrasexual disputes [6], the relationship between dominance and mate choice is far from clear [7]. Inconsistencies between species add additional confusion to the problem [8,9].

Central to the discussion on the evolution of status signalling within the context of social selection [10] is the understanding of which should be the frequency distribution of badge sizes. Rohwer and Ewald [11] proposed that bimodal distributions, with many birds either with large or small badges, but fewer individuals with intermediate badge sizes [12], should be quite common and could be maintained by negative frequency-dependent selection when individuals of different appearance and status either played mutually beneficial roles or employed alternate competitive tactics. However, although the Siskin (*Carduelis spinus*) has been found to display a bimodal distribution of badge sizes [13], the analysis of frequency distributions from most species reveals normality to be the rule [2,12,14]. Similar discussions appear in relation to characters seemingly evolved under sexual selection, where bimodal distributions are also predicted under certain mixed ESS [15], but again normal distributions are also quite common [16–18] (see Fig. 1). The subject can be further complicated by the interaction between social and sexual selection, although this has been rarely explored [2].

The aim of the present work is to use a hierarchical non-linear matrix model for the size distribution of badges of social status in natural (bird) populations, in order to predict evolutionarily stable equilibrium distributions under different hypotheses on parameters related to selection. Therefore, the goal is not to explore the dynamics itself of the signalling system, but to determine conditions for the evolutionary stability of the transition rates among classes (or ranks) under asymmetrical competition based on a system of status signalling with the hope that such conditions give clues of how a hierarchical or dominance ranking can be maintained. More precisely, assuming the honesty of the signalling system, individuals are categorized into discrete dominance classes according to the size of a given (plumage) trait which acts as a badge of social status. This size can increase and decrease over the lifetime of an individual by means of transitions between any pair of dominance classes (including reverse transitions). The dominance hierarchy is introduced by means of a negative class-specific dependence of the demographic rates on weighted sums of the population members. Such weighted sums are different for each dominance class and reflect the environmental conditions experienced by individuals in those classes. For instance, one can assume that subordinate individuals do not affect the environmental conditions experienced by those in the dominant classes, while dominant (and subdominant) individuals do affect the environment experienced by subordinates. An example of environmental condition can be the

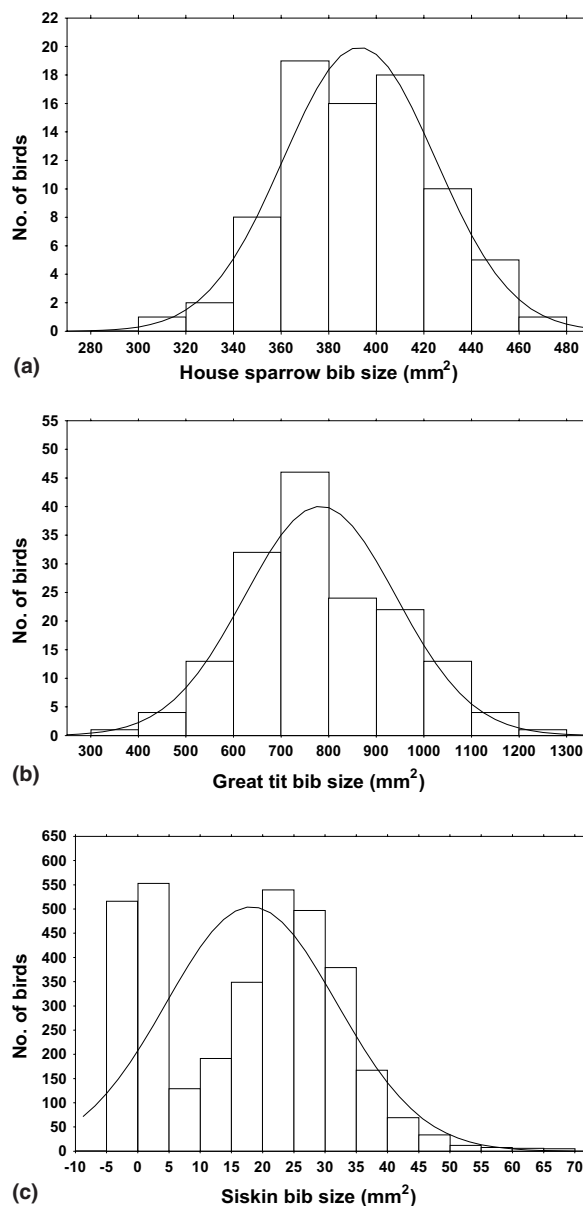


Fig. 1. Bib size frequency distribution in three species of birds for which the bib has been found to work as a signal of social status. Only data for males are used. (a) House sparrow (*Passer domesticus*); data and bib size measured according to [52]; Shapiro Wilk $W = 0.99$, $p = 0.91$, $N = 80$, 1983–1986. (b) Great tit (*Parus major*) [53]; bib size measured according to [51]; Shapiro Wilk $W = 0.99$, $p = 0.18$, $N = 160$, 1997–2000. (c) Siskin (*Carduelis spinus*); data and bib size measured according [20]; Shapiro Wilk $W = 0.93$, $p < 0.001$, $N = 3454$, 1990–2000; the class -5 to 0 refers to birds with a bib size of 0 mm². The mean and the variance of each fitted normal curve are the same as in the corresponding data.

average number of aggressive interactions per unit of time which, of course, is a function of the population composition.

A *strategy* in the model is given by a subset of probabilities of moving among classes. In particular, given the current state/class of an individual, it is assumed that natural selection acts to change the probabilities of moving from this state to any other state so as to maximize its fitness. Similarly to what is assumed in many metapopulation models where an optimal distribution of individuals in a patchy environment is pursued (see, for instance, [19,22]), in this adjustment by natural selection it is also assumed that individuals do not have information about the population composition so that they only experience their own environmental conditions in an average way as it could be, for instance, the total number of aggressive interactions they suffer per time interval. Other considerations as, for instance, considering an energetic cost of the transitions which affects the subsequent division of the energy between reproduction and maintenance, or introducing transition probabilities which are conditional on the actual population composition, lie outside of the scope of the present paper and will be considered in forthcoming research. In summary, premises of the present model are, first, to admit that it is convenient to change the expected time of residence in a given class in order to increase fitness, and, secondly, that this change is made by natural selection choosing optimal transition strategies and, so, assuming that individuals behave as if they have a ‘roulette wheel in their heads’ [19] when they randomly decide the transition for the next time period from a set of possible transitions according to the probabilities given by a transition matrix.

We use the Siskin as a model species, because of the fact of being the only species for which a bimodal status signalling system has been found [2]. The size of the black bib in this species is highly correlated to dominance [13], and manipulative experiments have shown that it functions as a reliable signal of dominance [20]. More importantly, the system seems to be independent of age, since both yearling and adult birds display either small or large badges and both yearlings and adults may be dominant or subordinate individuals [13]. Birds moult in autumn contour feathers, and as a consequence, the size of the black bib may increase or decrease in each moult (JCS, personal observation). We specifically test on the conditions favouring bimodality and normality in status signalling characters at equilibrium, taking into account population parameters such as survival rates, reproductive rate, and aggression rates. As we have already said, we do that from an evolutionary point of view taking as evolutionary variables the (vector of) probabilities of moving to other bib-size classes.

The paper is organized as follows. Section 2 introduces the matrix model, first presenting the linear problem and related concepts and hypotheses, and, afterwards, dealing with the full problem and the corresponding assumptions. The section ends with a bifurcation analysis to establish the existence of a unique positive equilibrium of the model and its (local) stability. A sufficient condition for the global stability of the extinction equilibrium is also given.

In the first part of Section 3 we obtain the evolutionarily singular transition probabilities for a general transition matrix by means of maximizing the *net reproductive number* here denoted by R_0 . This procedure allows us to see that the evolutionary stability of such a singular strategy of the adaptive dynamics is, in fact, neutral since it is not a strict local maximum of R_0 when adopted by the resident. In other words, R_0 turns out to be constant (and equal to 1) for any mutant when the resident, in demographical equilibrium, adopts the singular strategy. Since the transition matrix in the model is arbitrary, such a neutrality is also the case for the evolutionarily stable growth rates

obtained by Abrams in [21] under the assumption of a cost free growth in a size-dependent model. On the other hand, neutral singular strategies have been also obtained by Lebreton et al. in [22,23] when dealing with the problem of finding optimal dispersal strategies in discrete metapopulation models, and by Diekmann in [24,25] for the evolution of the timing of reproduction in semelparous species.

A singular strategy has the *ability to spread* as a mutant, property that is also called *invading potential*, when a small population of mutants (or invaders) adopting it can spread in a population at equilibrium where residents adopt a (nearby) strategy. Moreover, in case of neutral ESS-stability of the singular strategy, as in the present model, invading potential is equivalent to the so-called *convergence stability* of the singular strategy (see [26,27]). In the second part of Section 3 we numerically analyze such a property of the singular strategy. This study is made under particular assumptions about the survival and reproduction probabilities, which allows to obtain an explicit expression of the equilibrium when the parameter values define the evolutionarily singular strategy, even though the model is non-linear. Such an expression will become very useful for the simulations of invasion events. In particular, we will see that as long as competition effects within classes are stronger than those among classes (i.e., like-versus-like competition), the singular strategy turns out to be an evolutionarily stable strategy.

Section 4 is devoted to analyze which conditions on the parameters guaranteeing the existence of an evolutionarily singular strategy, also imply bimodality in the shape of the equilibrium. We recall again that this is one of our main purposes since, in case that such conditions exist, it could explain when bimodality is observed in nature and under which circumstances it appears instead of the more frequently observed unimodal equilibrium distributions.

Section 5 considers the particular situation in which only one-step transitions are allowed. In such a case, the transition matrix is tridiagonal and it is possible to obtain an explicit expression of R_0 , the net reproductive number. We use it to directly check the neutral stability of the singular strategy obtained in Section 3 for a general transition matrix.

Finally, Section 6 contains some remarks on the neutrality of the ESSs in optimization models, on the role of like-versus-like aggression in the so-called social control hypothesis, and on how bimodality in the size-distribution of badges can arise in species like the Siskin in which the plumage trait acts as a badge of status but does not have any role in mate choice.

2. Description of the model

2.1. The linear problem

If $N(t)$ denotes the n -class distribution vector at time t , the dynamics of a model as the one described before in a *virgin environment* (i.e., when competition effects are not present) is given by the following linear matrix equation

$$N(t+1) = \mathbf{P}N(t),$$

where, as usual, the $n \times n$ projection matrix \mathbf{P} decomposes as a sum of a *transition matrix* $\mathbf{T}_0 = (t_{ij})$ plus a *fecundity matrix* $\mathbf{F} = (f_{ij})$, i.e., $\mathbf{P} = \mathbf{T}_0 + \mathbf{F}$.

From now on we will assume the following hypotheses on the model ingredients:

(H1). For each time interval (census time, year), the transition probability t_{ij} from class j to a class i is given by

$$t_{ij} = \tau_{ij}s_j, \quad (1)$$

where, for each class j , $0 < s_j < 1$ is the survival probability of a j -class individual, and $\tau_{ij} \geq 0$ is the probability of moving from class j to class i . Since, *per* unit of time, any individual at any class either moves to another class or remains in the same, it follows that

$$\sum_{i=1}^n \tau_{ij} = 1,$$

for $j = 1, \dots, n$. The special form of the transition probabilities given by (1) allows us to express \mathbf{T}_0 as product of a stochastic matrix \mathbf{T} times a survival matrix \mathbf{S} in such a way that the projection matrix becomes

$$\mathbf{P} = \mathbf{TS} + \mathbf{F},$$

with $\mathbf{T} = (\tau_{ij})$ and $\mathbf{S} = \text{diag}(s_1, \dots, s_n)$.

(H2). Newborns are assumed to lie in the subordinate class (1-class), i.e., $\mathbf{F} = (f_{ij})$ with $f_{1j} = f_j > 0$ and $f_{ij} = 0$ for $i = 2, \dots, n, j = 1, \dots, n$. Reproduction occurs at the beginning of the time period which implies that the contribution of the j -class to the 1-class is given by the term $f_j N_j$.

(H3). The projection matrix \mathbf{P} is primitive. Under hypotheses (H1) and (H2) a sufficient condition for primitivity of \mathbf{P} is $\tau_{i+1,i} > 0$ for all i (see [28]).

Under the previous hypotheses, \mathbf{P} is a non-negative matrix and, by means of the Perron–Frobenius theorem, it has a simple and strictly dominant eigenvalue $\lambda_1 > 0$ with strictly positive left and right eigenvectors, \mathbf{u} and \mathbf{v} , respectively (see [29]). Therefore, the dynamics of the model is given by the so-called Fundamental Theorem of Demography which says that, at the long run, the total population grows like λ_1^t and its normalized class-distribution tends to the so-called *stable distribution* which is given by the normalized right eigenvector corresponding to λ_1 , $\mathbf{v}/\|\mathbf{v}\|$ (see [28]). Hence, the population will go extinct if $\lambda_1 < 1$ and grows exponentially without bound if $\lambda_1 > 1$.

2.1.1. The net reproductive number R_0

Another important quantity which, under certain hypotheses, is equivalent to predict the asymptotic behaviour of the linear model is the so-called *net reproductive number*, also called *basic reproduction number*, and usually denoted by R_0 in epidemiology and life history theory. This number is defined as the individual expected production of offspring per lifetime and, when newborns belong to a single class, the strictly dominant eigenvalue of the matrix $\mathbf{R} := \mathbf{F}(\mathbf{I} - \mathbf{T}_0)^{-1}$ corresponds exactly to R_0 .

The equivalence between λ_1 and R_0 to describe the long term behaviour of linear matrix models is given by the fact that, under hypotheses (H1)–(H3), one of the following relationships holds: $\lambda_1 = R_0 = 1$ or $0 < R_0 < \lambda_1 < 1$ or $1 < \lambda_1 < R_0$ (see [28,30]). Therefore, the population will go extinct if $R_0 < 1$ and grows exponentially without bound if $R_0 > 1$.

The matrix \mathbf{R} is called the *next generation matrix* since it projects the population from one generation to the next, and its strictly dominant eigenvalue R_0 gives the growth rate of the population from one generation to the next (see [29]). Precisely, since the fecundity matrix \mathbf{F} only has entries different from zero in the first row, only the first row of \mathbf{R} is non-zero with $r_{1j} > 0$ for all j . Hence, \mathbf{R} has a positive simple strictly dominant eigenvalue $R_0 = r_{11}$, and the other $(n - 1)$ eigenvalues are equal to zero. In the model, the existence of the matrix \mathbf{R} is guaranteed because the elements of \mathbf{T}_0 satisfy $\sum_{i=1}^n t_{ij} = \sum_{i=1}^n \tau_{ij}s_j = s_j < 1 \ \forall j$, which is a sufficient condition for the existence of $(\mathbf{I} - \mathbf{T}_0)^{-1}$ (see [28]).

Note that the existence of a positive, simple, and strictly dominant eigenvalue R_0 of the matrix \mathbf{R} is guaranteed by the fact that only one row of \mathbf{F} is non-zero and, so, it does not depend on the primitivity of the projection matrix \mathbf{P} , i.e., it does not depend on the existence of a positive, simple, and strictly dominant eigenvalue λ_1 of \mathbf{P} . This implies that it is possible to have generational stability ($R_0 = 1$) but, at the same time, permanent oscillations of the normalized class-distribution which appear when \mathbf{P} is irreducible but imprimitive and $\lambda_1 = 1$ is a dominant but not strictly dominant eigenvalue (see [30] for a discussion and examples).

On the other hand, since the (i, j) -entry in $(\mathbf{I} - \mathbf{T}_0)^{-1}$ gives the expected number of time steps spent in class i by an individual starting life in class j , the element r_{1j} of \mathbf{R} gives the expected lifetime production of newborns of an individual starting life in class j . Hence the dominant eigenvalue R_0 of \mathbf{R} has the interpretation given above, namely, the expected number of offspring produced by an individual during its lifetime, as long as there is a only offspring class. However, when this is not the case, i.e., there are more than one offspring classes, this interpretation of R_0 is no longer valid, though it remains true that R_0 corresponds to the generation growth rate (see [29] for a discussion).

To deal with R_0 , instead of computing the matrix $(\mathbf{I} - \mathbf{T}_0)^{-1}$, which is not easy when the complexity of \mathbf{T}_0 increases, from now on we will consider the system of linear equations

$$\mathbf{R}(\mathbf{I} - \mathbf{T}_0) = \mathbf{F}. \tag{2}$$

2.1.2. Reproductive value

The sum of all the contributions to reproduction from stage i to the (last) stage n is the *reproductive value of class i* . In matrix population models, the left eigenvector \mathbf{u} of the projection matrix associated to the dominant eigenvalue λ_1 is interpreted as a measure of these reproductive values [29]. In fact, it is immediate to see that if \mathbf{u} is a left eigenvector of \mathbf{P} corresponding to λ_1 , $\mathbf{u}'\mathbf{P} = \lambda_1\mathbf{u}'$, then \mathbf{u} is a left eigenvector of $\mathbf{R}_{\lambda_1} := \mathbf{F}(\lambda_1\mathbf{I} - \mathbf{T}_0)^{-1}$ corresponding to the eigenvalue 1.

Therefore, when $\lambda_1 = 1$, $\mathbf{R}_{\lambda_1} = \mathbf{R}$ and $R_0 = 1$. In this case, $\mathbf{u}'\mathbf{P} = \mathbf{u}'\mathbf{R} = \mathbf{u}'$ which implies that the vector of reproductive values is proportional to the first row of \mathbf{R} , i.e., $\mathbf{u}' = \alpha(r_{11}, \dots, r_{1n})$. In particular, normalizing \mathbf{u} by α and since $r_{11} = 1$, it follows that $\tilde{\mathbf{u}} = (1, r_{12}, \dots, r_{1n})$ is a left eigenvector of \mathbf{P} and \mathbf{R} corresponding to the eigenvalue 1. This fact will be used in the next sections to give an interpretation of the results we will obtain.

2.2. The non-linear problem

To introduce the effects of population density (i.e., non-linearities) in structured populations models it is usually assumed a dependence of the vital rates (mortality, survival and reproduction)

on certain population variables in such a way that, when their values are prescribed, models become linear, that is, individuals are independent from each other. Such variables are sometimes called *interaction variables*, ϕ_k , and constitute the environmental feedback: environmental conditions are determined by the population distribution and, in its turn, this biotic environment determine the interactions among individuals (see [31]). When symmetric competition is assumed, these interaction variables ϕ_k are *weighted total population sizes* and they are the same for any member of the population. However, when dealing with hierarchical models in which asymmetric competition among individuals is assumed, the interaction variables can be weighted sums of the number of individuals of only certain classes, i.e., they can be functionals of the population class-distribution $N(t)$, and moreover they are different for different classes (see [28] for examples).

In order to introduce the environmental feedback in the population dynamics of the model, we will consider density effects in both fecundity elements and survival probabilities. In particular we will assume the following hypotheses:

(H4). The i -class survival probability, s_i , and the i -class fecundity rate, f_i , are continuous and strictly decreasing functions of $\phi_i(N)$ with $\phi_i(N) \neq \phi_j(N)$ if $i \neq j$, and tending to 0 as $\phi_i(N) \rightarrow \infty$. Moreover, for any class i , the inherent or maximal survival probabilities and the inherent or maximal fertilities, denoted by s_i^0 and f_i^0 respectively, satisfy the inequality

$$s_i^0 + f_i^0 > 1, \quad i = 1, \dots, n. \quad (3)$$

(H5). The functions $\phi_i(N)$, $i = 1, \dots, n$, are weighted sums of the number of individuals at each class. More precisely, $\phi_i(N)$ are of the form

$$\phi_i(N) = \sum_{j=1}^n w_{ij} N_j, \quad i = 1, \dots, n,$$

with $\mathbf{W} = (w_{ij})$ a *non-negative invertible* matrix.

In terms of the projection matrix, (H4) means that the density effects are included in the fecundity and survival matrices and the model becomes non-linear and reads

$$N(t+1) = (\mathbf{TS}(N(t)) + \mathbf{F}(N(t)))N(t), \quad (4)$$

where the dependence of \mathbf{S} and \mathbf{F} on N is by means of $\Phi = (\phi_1, \dots, \phi_n) \geq 0$, the vector of interaction variables.

In turn, the hypothesis on \mathbf{W} in (H5) guarantees the existence and uniqueness of a population distribution \tilde{N} for a given Φ since then $\tilde{N} = \mathbf{W}^{-1}\Phi$. Roughly speaking, this is equivalent to say that, given certain environmental conditions as described by a vector of interaction variables Φ , there exists only one population distribution causing them.

The values of the weights w_{ij} determine what sort of environment is experienced by each dominance class. For instance, if, for a given i , one assumes that coefficients of the weighted averages satisfy $w_{i1} < \dots < w_{in}$, this means that contributions of individuals in higher classes to the density effects experienced by individuals in class i (the environment of the i -class) are more important than those of individuals in lower classes.

In fact, the choice of the weights w_{ij} is a way to introduce *dominance hierarchy* in the social structure of the population, i.e., a disproportionate share of the resources by the *dominants*, in our

case, the individuals of the biggest bib-size class. To see this fact, let us consider two dominance classes, i and j , and the corresponding reciprocal contributions to the environment experienced by them, namely, w_{ij} and w_{ji} . Whenever $w_{ij} < w_{ji}$, the contribution to the experienced environment by class i by individuals of class j is lower than that of individuals of class i to the environment of class j . In this case, class i is dominant to class j .

Such a dominance hierarchy appears many times by means of aggressive interactions among individuals of the same class (intra-class aggressions) and among individuals of different classes (inter-class aggressions). In such cases, w_{ij} can be thought of as the mean number of aggressive interactions that an individual of class i suffers from an individual of class j per time interval. Normalizing the number of aggressive interactions by the total number of *per capita* aggressions experienced by an i -class individual per time unit ($\sum_j w_{ij}$), the entry w_{ij} of \mathbf{W} would represent the probability that an individual of class i suffers an aggression from an individual of class j per time period and, so, it satisfies $0 \leq w_{ij} \leq 1$ with $\sum_j w_{ij} = 1$ for $i = 1, \dots, n$. In such a case, $\phi_i(N)$ gives the *expected number of aggressions experienced by an individual of class i during a time interval* when the class distribution in the population is given by N , which is clearly a measure of the competition effects (environment) experienced by those members belonging to the i -class. Under this interpretation of w_{ij} , individuals of class i dominate individuals of class j if the (mean) number of aggressions suffered by an i -class individual per time interval and per j -class individual is lower than the (mean) number of aggressions suffered by a j -class individual per time interval and per i -class individual.

2.2.1. Stationary solutions

A positive stationary solution or equilibrium of the model is a positive time-invariant solution of the ecological dynamics governed by (4), i.e., a solution $N^* > 0$ of the non-linear equation

$$N^* = \mathbf{P}(N^*)N^* = (\mathbf{TS}(N^*) + \mathbf{F}(N^*))N^*. \tag{5}$$

Since, under (H1)–(H3), the projection matrix at the equilibrium, $\mathbf{P}(N^*)$, is assumed to be non-negative and primitive, to say that $N^* > 0$ is an equilibrium of (4) is equivalent to say that N^* is a positive right eigenvector of $\mathbf{P}(N^*)$ corresponding to the eigenvalue 1. In particular, under (H3), this implies that $\lambda_1 = 1$ has to be a strictly dominant eigenvalue of $\mathbf{P}(N^*)$ with a strictly positive right eigenvector \mathbf{v} which is proportional to N^* , and with a strictly positive left eigenvector \mathbf{u} , proportional to the first row of the next generation matrix $\mathbf{R}(N^*)$, which is also a left eigenvector of $\mathbf{R}(N^*)$ belonging to the eigenvalue 1. Hence, it also follows that $R_0(N^*) = 1$ (see Subsection 2.1.2).

On the other hand, $N^* \equiv \mathbf{0}$ is always a solution to (5) and, so, an equilibrium of (4), and it satisfies the following

Lemma 1. *Under hypotheses (H4) and (H5) the extinction equilibrium $N^* \equiv \mathbf{0}$ of (4) is always unstable.*

Proof. As s_i and f_i are assumed to be continuous and strictly decreasing functions of $\phi_i(N)$, there exists $\varepsilon_0 > 0$ such that, for all i , $s_i(\varepsilon) + f_i(\varepsilon) > 1 \ \forall \varepsilon < \varepsilon_0$. Let us consider an arbitrary initial population $N(0)$ such that $\phi_i(N(0)) < \varepsilon_0$ for all i . Then, adding up the n equations of (4), it follows that, for $t = 1$,

$$\sum_i N(1) = \sum_i [s_i(N(0)) + f_i(N(0))]N_i(0) > \sum_i N_i(0),$$

which means that the total size of small enough populations increases with t as long as their weighted sizes $\phi_i(N(t))$ are lower than ε_0 for all i . Hence the instability of $\mathbf{0}$ follows, i.e., $\lambda_1(\mathbf{0}) > 1$. \square

This fact allows us to prove the following

Theorem 1. *Under hypotheses (H1)–(H5) there exists an equilibrium $N^* > 0$ of (4).*

Proof. Under (H4) all the entries of $\mathbf{P}(N)$ are strictly decreasing functions of ϕ_i for some i , and tending to zero as $\phi_i \rightarrow \infty$ for all i . Moreover, under (H5), such entries tend to zero as $N_i \rightarrow \infty$ for all i . Hence, from the Perron–Frobenius theorem, it follows that the spectral radius of $\mathbf{P}(N)$, $\rho(\mathbf{P}(N)) = \lambda_1(N)$, decreases (strictly) with ϕ_i for any $i \in [1]$ with $\lambda_1(N) \rightarrow 0$ as $N_i \rightarrow \infty$ for all i since then $\|\mathbf{P}(N)\| \rightarrow 0$ and the spectral radius satisfies $\rho(\mathbf{P}) \leq \|\mathbf{P}\|$ (see [30]). Finally, from the previous Lemma, $\lambda_1(\mathbf{0}) > 1$ and, hence, the existence of a value $N^* > 0$ such that $\lambda_1(N^*) = 1 < \lambda_1(\mathbf{0})$ follows. \square

Theorem 2. *If (3) is replaced by $s_i^0 + f_i^0 < 1 \forall i$ in (H4), the extinction equilibrium is globally stable under hypotheses (H1)–(H5).*

Proof. The stability of the extinction equilibrium trivially follows because

$$\lambda_1(\mathbf{0}) < \|\mathbf{P}(\mathbf{0})\|_1 := \max_j \sum_i (\tau_{ij}s_j^0 + f_j^0) = \max_j \{s_j^0 + f_j^0\} < 1.$$

Moreover, using similar arguments as in the proof of the previous theorem, it follows the non-existence of an equilibrium $N^* > 0$ since there is no vector $N > 0$ for which $\lambda_1(N) = 1$. In fact, monotonicity hypotheses in (H4) and the condition on the parameters of the lemma imply global extinction, i.e., $N(t) \rightarrow \mathbf{0}$ as $t \rightarrow \infty$ for all $N(0) > 0$, since $\lambda_1(N) < \lambda_1(\mathbf{0}) < 1$ for all $N > 0$ (see [28] for details). \square

If $s_i^0 + f_i^0 > 1$ for some i , while $s_j^0 + f_j^0 < 1$ for $j \neq i$, the instability of the extinction equilibrium is not guaranteed and a detailed analysis is needed to establish conditions for the existence of an equilibrium $N^* > 0$. In particular, note that $f_1^0 > 1$ is a sufficient condition for the instability of the trivial equilibrium since $\rho(\mathbf{P}(\mathbf{0})) > \rho(\mathbf{F}(\mathbf{0})) = f_1^0$.

As usual in applications of matrix models in population dynamics, we can use $R_0(\mathbf{0})$ as a bifurcation parameter since it follows that $0 < R_0(\mathbf{0}) < \lambda_1(\mathbf{0}) < 1$ if $s_i^0 + f_i^0 < 1 \forall i$, and $1 < \lambda_1(\mathbf{0}) < R_0(\mathbf{0})$ if $s_i^0 + f_i^0 > 1 \forall i$. In fact, for continuity with respect to the parameters of the model, $R_0(\mathbf{0})$ attains the critical value $R_0^c = 1$ for $s_i^0 + f_i^0 = 1$ ($i = 1, \dots, n$), even though other combinations of parameters giving $R_0(\mathbf{0}) = 1$ are possible.

Note that, under (H4) and (H5), the entries of $\mathbf{P}(N)$ are non-increasing functions of N_i , $i = 1, \dots, n$, which are strictly decreasing for at least some i . Hence, from bifurcation theory in discrete dynamical systems (see Theorems 1.2.5 and 1.2.6 in [28]), the next result follows:

Theorem 3. (Supercritical bifurcation): *Under hypotheses (H1)–(H5) and assuming that $s_i = s_i(s_i^0, N)$ and $f_i = f_i(f_i^0, N)$ are \mathcal{C}^k -functions, $k \geq 2$, there exists a continuum C^+ of equilibrium pairs $(R_0(\mathbf{0}), N^*)$ with $(1, \mathbf{0}) \in C^+$ and containing only positive equilibria for $R_0(\mathbf{0}) > 1$. Moreover, in a sufficiently small neighbourhood of the bifurcation point $(1, \mathbf{0})$, there exists a unique equilibrium $N^* > 0$ for each value $R_0(\mathbf{0}) > 1$ which is locally asymptotically stable, whereas the extinction equilibrium is unstable.*

Corollary. *Under the hypotheses of Theorem 3, the equilibrium $N^* > 0$ of (4) is (locally) asymptotically stable for $s_i^0 + f_i^0 > 1$ near 1 for all i , whereas the extinction equilibrium is unstable.*

Remarks

- (i) According to the theory of positive matrices (see, for instance, [29], Chapter 4), if there exists a non-negative stationary solution N^* which is not strictly positive (i.e., $N_j^* = 0$ for some j), this means that (H3) does not hold and, in particular, that $\mathbf{P}(N^*)$ is reducible and, so, the existence of a strictly dominant eigenvalue is not guaranteed. It is well-known that this fact depends on the pattern of $\mathbf{P}(N^*)$ and, since the pattern of $\mathbf{F}(N^*)$ is given and $\mathbf{S}(N^*)$ is diagonal, it only depends on the pattern of \mathbf{T} . In such a situation, however, the vector of reproductive values, which is the left eigenvector of \mathbf{R} which belongs to $R_0 = 1$, is still strictly positive as R_0 is a strictly dominant eigenvalue of \mathbf{R} . When this is the case, it follows that $\rho(\mathbf{P}) = R_0 = 1$ or $1 < \rho(\mathbf{P}) \leq R_0$ or $0 \leq R_0 \leq \rho(\mathbf{P}) < 1$ (see [30]).
- (ii) One can introduce R_0 explicitly in the model (4) by scaling the fecundity matrix to R_0 . In such a case, we have $f_{ij} = R_0 \psi_{ij}$ and $\mathbf{P} = \mathbf{TS} + R_0 \mathbf{\Psi}$ with $\mathbf{\Psi} = (\psi_{ij})$. With this normalized fecundity matrix, it follows that $\rho(\mathbf{TS} + \mathbf{\Psi}) = 1$ if $R_0 > 0$ (see [28,30]).

3. Adaptive dynamics

3.1. Preliminaries

From an evolutionary point of view, we consider that individuals are characterized by a (multi-dimensional) variable specifying relevant aspects of the life history (according to our interests) in which they may differ. Consequently, the values of this variable are submitted to natural selection and, for this reason, it is called *evolutionary trait* or *variable*. A particular value of it is called *type* or, more generally, *strategy*. In our case, this evolutionary variable is given by a vector η of dimension less than or equal to $n(n - 1)$ and formed by a subset of transition probabilities τ_{ij} .

Due to the existence of a linear restriction on the elements of each column of \mathbf{T} (namely, $\sum_i \tau_{ij} = 1 \forall j$) and in order to have a well-posed optimization problem (see below), the set of possible strategies has to be restricted to a subset of admissible strategies.

Definition. A vector η of dimension $l \leq n(n - 1)$, is said to define an *admissible strategy* if

- (a) The whole of the (non-zero) entries of any column of $\mathbf{T} = (\tau_{ij})$ is not included among the components of η ,

- (b) For every $i \in \{1, 2, \dots, n\}$ there exists at least one $j \in \{1, 2, \dots, n\}$ such that $\tau_{ij} > 0$ and either τ_{ij} is a component of η or there is another element τ_{kj} , $k \neq i$, of the same column of \mathbf{T} which is a component of η .

The first condition excludes linear dependencies among the elements of η and, hence, it allows us to do without Lagrange multipliers in the optimization procedure below. The second condition assures that all the (dominance) classes are affected by the transitions defining the strategy vector η . For instance, this is the case when the strategy is given by the growth rates in discrete size-structured models [21], or when the strategy is given by the dispersal rates in discrete metapopulation models with a ‘full’ dispersal matrix [22,23]. In general, however, one has to be precise with respect to the choice of the transitions in order to have a well-defined optimization problem (see the proof of Theorem 4 below).

More precisely, in a standard size-structured matrix model we have the following transition matrix

$$\mathbf{T} = \begin{pmatrix} 1 - \eta_1 & 0 & 0 & \dots & 0 & 0 \\ \eta_1 & 1 - \eta_2 & 0 & \ddots & 0 & 0 \\ 0 & \eta_2 & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \ddots & \ddots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & 1 - \eta_{n-1} & 0 \\ 0 & 0 & 0 & \dots & \eta_{n-1} & 1 \end{pmatrix},$$

with $\eta = (\eta_1, \dots, \eta_{n-1})$ the only admissible strategy. In fact, if $n \geq 3$, the strategy $\eta = (\eta_1, \dots, \eta_{n-2})$ is not admissible because there is no component of the strategy vector η directly affecting the class n . Another example of an admissible strategy is given by $\eta = (\tau_{1j}, \dots, \tau_{n-1,j})$ where $\mathbf{T} = (\tau_{ij})$ is a $n \times n$ transition matrix without zero entries, since then the column j is also ‘full’ and, so, its entries define transitions from class j to *any* other class. Finally, another example is given by the case we have called ‘the dilemma of the subdominants’ in Subsection 3.3. In this case, \mathbf{T} is a 3×3 primitive matrix with the second column being the only full column and with $\eta = (\tau_{12}, \tau_{32})$. In both examples, any change in η directly affects all classes in the life histories of the individuals.

In the following, we will make a rather restrictive assumption on the (ecological) dynamics of the model, namely, the existence of a globally asymptotically stable equilibrium $N^* > 0$ for all positive initial condition $N(0)$. This assumption allows for supposing that, before the arrival of a mutant, the resident population has come to a steady state, which is the usual setting in most of the analysis in adaptive dynamics [24,27,31–33]. In fact, though it is well-known that discrete models usually show complicated dynamics under a suitable selection of parameters [28], especially when exponential non-linearities are considered as in Subsection 3.3, the previous assumption of global stability of N^* is in agreement with what we have observed in all the numerical simulations as long as (3) holds with its LHS close enough to 1 for all i (recall that we already saw in Section 2 that, in this case, $N^* > 0$ appears as a consequence of a supercritical bifurcation from the extinction equilibrium). Otherwise, assuming high enough fecundity rates, N^* becomes unstable and periodic orbits appear.

Since the resident population is assumed to be at equilibrium, we can use R_0 as a fitness measure to analyze the success of invasion events. For a fixed $l \leq n(n - 1)$, let Ω be the trait space, i.e., the

set of all possible non-negative values of the strategy vector η . The adaptive dynamics (AD) of the model will be given by trajectories in Ω defined by trait substitution sequences. Steady strategies of the AD are called *evolutionarily stable (or steady) strategies* (ESS) [25,26]. By assuming infinitesimal mutational steps, the AD is described by a deterministic limit equation called *canonical equation* [27,33,34]. This equation accounts both for the mutational process – described by a covariance (or mutational) matrix – and for the action of natural selection – by means of the so-called fitness gradient. Rest points of this equation correspond to *singular strategies*.

It is well-known from the modern theory of adaptive dynamics that the (local) *ESS-property* of a singular strategy, i.e., immunity of the resident adopting it in front of any new (nearby) strategy, called mutant or invader, is not a dynamic concept. The reason is that its definition does not imply its evolutionary attractiveness, i.e., it does not imply that the substitutions of types (strategies) occurring during the course of evolution lead to the establishment of such a singular strategy. This fact, indeed, is related to the concept of *convergence stability* (a singular strategy is said to be (locally) convergence stable if a resident type having a (nearby) strategy can be invaded by mutants adopting an even closer strategy). In other words, convergence stable singular strategies correspond to asymptotically stable equilibria of the canonical equation of the AD [27,34]. This property and the (local) ESS-property are two totally independent stability concepts that can occur in any combination. In fact, a convergence stable strategy which is also evolutionarily stable is called *continuously stable strategy* [26].

Another property that a singular strategy can have is the *ability to spread* in populations adopting slightly different strategies, a property that is also called *invading potential*. In particular, a singular strategy that is evolutionarily stable and that has the ability to spread as mutant strategy is also necessarily convergence stable, i.e., such a singular strategy is an attractor of the corresponding adaptive dynamics.

In a one-dimensional trait space, this equivalence of properties is easily seen from the so-called pairwise invasibility plot [26]. For multidimensional traits and using R_0 as a fitness measure, a sufficient condition for a singular strategy η^{ss} to be convergence stable is that the following matrix

$$\left[\frac{\partial^2 R_0(\eta^{inv}, \eta^{res})}{\partial \eta_i^{inv} \partial \eta_j^{inv}} \right]_{\eta^{inv}=\eta^{res}=\eta^{ss}} - \left[\frac{\partial^2 R_0(\eta^{inv}, \eta^{res})}{\partial \eta_i^{res} \partial \eta_j^{res}} \right]_{\eta^{inv}=\eta^{res}=\eta^{ss}} \quad (6)$$

is negative definite, where η^{res} denotes the strategy adopted by the resident which is assumed to be at population dynamical equilibrium, and η^{inv} denotes the strategy adopted by the invader [27,34]. Therefore, since evolutionary stability of the singular strategy implies that the first matrix is negative definite, and the invading potential implies that the second matrix has to be positive definite, the condition for the convergence stability is fulfilled when the singular strategy has both previous properties (see [27,34] for details).

In matrix games, for instance, a restriction appears in the combination of these properties as the fitness function is linear in the mutant strategy. A similar situation occurs in population dynamics if the fitness function becomes constant for any mutant strategy when the resident, in demographical equilibrium, adopts the singular strategy. In both cases, the singular strategy does not define a strict maximum of the fitness measure. Hence, it follows that *the condition for having an invading potential implies the convergence stability of the singular strategy* as the first matrix in (6)

is equal to the null matrix and, then, invading potential is a sufficient condition for convergence stability.

Note that, since the elements of the transition matrix \mathbf{T}_0 are given by (1), at the equilibrium N^* , \mathbf{T}_0 is a function of both the strategy η and the distribution population vector at equilibrium N^* , which is itself a function of the resident strategy. More precisely, the dependence of \mathbf{T}_0 on η^{inv} and η^{res} has the form

$$\mathbf{T}_0 = \mathbf{T}(\eta^{\text{inv}})\mathbf{S}(N^*(\eta^{\text{res}})).$$

Therefore, as R_0 is the dominant eigenvalue of $\mathbf{R} = \mathbf{F}(\mathbf{I} - \mathbf{T}_0)^{-1}$, it follows that the dependence of R_0 on the second argument in (6) is through N^* , i.e.,

$$R_0(\eta^{\text{inv}}, \eta^{\text{res}}) = R_0(\eta^{\text{inv}}, N^*(\eta^{\text{res}})).$$

3.2. Singular strategies

The success of an invasion process can be analyzed by means of the ESS concept. The fitness of an invader adopting η^{inv} at a demographic equilibrium of a resident adopting η^{res} is given by $R_0(\eta^{\text{inv}}, N^*(\eta^{\text{res}}))$ where, as before, $N^*(\eta)$ denotes the equilibrium distribution of a resident adopting the strategy η . A strategy η^{ESS} is said to be an ESS if the mapping

$$\eta \rightarrow R_0(\eta, N^*(\eta^{\text{ESS}}))$$

is maximal at $\eta = \eta^{\text{ESS}}$ (see [31]). That is, a (local) ESS is a strategy such that, when it is adopted by the resident, no mutant or invader with another (nearby) strategy can spread.

In general, if a fitness measure is differentiable with respect to η , we say that a strategy $\eta^{\text{SS}} \in \text{int}\Omega$ is a *singular strategy* if the gradient of this fitness measure evaluated at the demographic equilibrium of resident adopting it is equal to zero at this strategy (in our case, $\nabla_{\eta}R_0(\eta, N^*(\eta^{\text{SS}}))|_{\eta=\eta^{\text{SS}}} = \mathbf{0}$). Therefore, since by definition of ESS the fitness measure (here R_0) has a local maximum at such an strategy, the fitness gradient at an interior ESS is zero, which means that an interior ESS is a singular strategy of the adaptive dynamics. When this maximum is not strict, then there exists a neighbourhood of the singular strategy $U(\eta^{\text{SS}})$ such that all strategies in it render mutants (invaders) with the same fitness as the resident, i.e., $R_0(\eta, N^*(\eta^{\text{SS}})) = 1$ for all $\eta \in U(\eta^{\text{SS}})$. When this is the case, the singular strategy presents what is called a *neutral evolutionary stability*.

Of course, one can ask about the existence of strategies at the boundary of the trait space, $\partial\Omega$, for which the fitness gradient needs not to be zero but, even so, the fitness measure has a local maximum, i.e., boundary ESSs. To answer this question one has to compute the signs of the components of $\nabla_{\eta}R_0(\eta, N^*(\eta^b))|_{\eta=\eta^b}$ with $\eta^b \in \partial\Omega$ in order to see if $\partial\Omega$ acts as an attractor or as a repeller of the AD (see [25] for an example in a one-dimensional trait space). However, numerical simulations of the two-dimensional AD of the model show that, as long as an interior singular strategy has invading potential, such a property holds for any (nearby or not) resident strategy. This fact, plus the global and neutral evolutionary stability of the singular strategy (see below), amounts to the global attractiveness of such a strategy. Otherwise, it would exist a one-dimensional path in Ω along which the singular strategy is able to spread but is not convergence stable, which would contradict the equivalence between such properties in one-dimensional AD when the singular strategy is globally evolutionary neutral [26]. Therefore, conditions for an invading po-

tential will guarantee the global convergence stability of the interior ESS. For this reason, from now on we will only consider interior fixed points of the AD.

Theorem 4. *Under hypotheses (H1)–(H5) and assuming the existence of a globally stable positive equilibrium of the non-linear model (4), there exists a set of evolutionarily singular strategies of the adaptive dynamics associated to the model which define a unique equilibrium population $N^*(\eta^{ss})$. Moreover, all these singular strategies are characterized by a neutral evolutionary stability.*

Proof. Let τ_{km} be a component of an admissible strategy η and consider another element of the same column $\tau_{lm} \neq 0$ with $l \neq k$. We know that such an element exists since, otherwise, $\tau_{km} = 1$. Moreover, let $N^*(\eta^{ss})$ be the equilibrium defined by the singular strategy η^{ss} , and $s_i^* = s_i(N^*(\eta^{ss}))$ and $f_i^* = f_i(N^*(\eta^{ss}))$ ($i = 1, \dots, n$). Using that $\tau_{lm} = 1 - \sum_{q \neq l} \tau_{qm}$, and differentiating (2) with respect to τ_{km} , one obtains the following linear system in $\frac{\partial r_{li}}{\partial \tau_{km}}$, $i = 1, \dots, n$:

$$\sum_{i=1}^n (\delta_{im} - t_{im}) \frac{\partial r_{li}}{\partial \tau_{km}} = s_m^* (r_{lk} - r_{ll}), \tag{7}$$

$$\sum_{i=1}^n (\delta_{ij} - t_{ij}) \frac{\partial r_{li}}{\partial \tau_{km}} = 0 \quad (j \neq m), \tag{8}$$

where δ_{ij} is the Kronecker delta.

Since, at the singular strategy, $\partial r_{11} / \partial \tau_{km} = 0$, (8) is a homogeneous system of $n - 1$ equations with $n - 1$ unknowns. On the other hand, since $\mathbf{I} - \mathbf{T}$ is non-singular and the matrix of (8) is obtained by deleting row m and column 1 of the transpose of $\mathbf{I} - \mathbf{T}$, it follows that (8) is a non-singular homogeneous system and, so, it only has as a solution the trivial one, that is,

$$\frac{\partial r_{li}}{\partial \tau_{km}} = 0, \quad i = 2, \dots, n. \tag{9}$$

Hence, in order to fulfill (7), it follows that $r_{lk} = r_{ll}$ for all $l \neq k$ such that $\tau_{lm} \neq 0$.

Computing the derivative of (2) with respect to the rest of the components of η and using the condition of singular strategy, namely,

$$\text{for all } \tau_{ij} \text{ in the strategy } \eta, \quad \frac{\partial R_0}{\partial \tau_{ij}} = \frac{\partial r_{11}}{\partial \tau_{ij}} = 0,$$

(7) and (8) imply that, at the equilibrium determined by the singular strategy, the elements of the first row of \mathbf{R} satisfy

$$r_{11} = r_{12} = \dots = r_{1n} = 1. \tag{10}$$

Notice that the fact that η is an *admissible strategy* guarantees that this condition holds for all r_{li} . Otherwise, some of the elements of the first row of \mathbf{R} would remain undetermined. This means that, if η were not admissible, there would be unaffected reproductive values by the maximization of the fitness measure or, in other words, there would be unaltered stages of the life history of the individuals when we change the strategy η , which is clearly unsatisfactory.

Substituting (10) in (2) it follows immediately that, to be a singular strategy, η has to render an equilibrium N^* fulfilling the condition

$$s_i^* + f_i^* = 1, \quad i = 1, \dots, n. \tag{11}$$

Note that (H4) and (H5) guarantee the existence of a unique equilibrium $N^* > 0$ satisfying (11), and that the number of strategies rendering such an equilibrium depends on the dimension of strategy. In particular, if the dimension of η is less than n then the singular strategy will be uniquely determined from (5) and (11).

To see whether $\eta \rightarrow R_0(\eta, N^*(\eta^{ss}))$ is maximal at $\eta = \eta^{ss}$ or not, we can differentiate (7) and (8) with respect to τ_{km} , τ_{km} a component of the strategy vector η , as many times as we need. Using (9), it follows directly that

$$\frac{\partial^i R_0}{\partial \tau_{km}^i}(\eta^{ss}, N^*(\eta^{ss})) = 0, \quad i = 2, 3, \dots$$

for any τ_{km} in the strategy η . That is, the singular strategy does not define a strict maximum of the mapping $\eta \rightarrow R_0(\eta, N^*(\eta^{ss}))$. In fact, we can easily obtain more information about this mapping by computing $R_0(\eta^{inv}, N^*(\eta^{ss}))$ with $\eta^{inv} \neq \eta^{ss}$.

Eq. (2) corresponding to an invader adopting a strategy η^{inv} , which determines a transition matrix \mathbf{T}^{inv} , when the resident adopts η^{ss} is

$$\mathbf{R}^{inv}(\mathbf{I} - \mathbf{T}^{inv}\mathbf{S}^*) = \mathbf{F}^*,$$

where \mathbf{S}^* and \mathbf{F}^* are the survival and the fecundity matrices at the equilibrium $N^*(\tau^{ss})$, respectively. However, since $\mathbf{T}^{inv} = (\tau_{ij}^{inv})$ is a stochastic matrix, it follows that, for all j , $\sum_i \tau_{ij}^{inv} s_j^* = s_j(N^*(\eta^{ss}))$. Therefore, in order to fulfill (2) and since s_i^* and f_i^* satisfy (11), \mathbf{R}^{inv} must be equal to \mathbf{R}^* , the matrix \mathbf{R} of the resident adopting the singular strategy, which implies that

$$R_0(\eta^{inv}, N^*(\eta^{ss})) = 1,$$

for any (nearby or not) admissible strategy η^{inv} adopted by the invader. That is, the mapping $\eta \rightarrow R_0(\eta, N^*(\eta^{ss}))$ is constant and equal to 1. \square

In other words, we have seen that *under the equilibrium conditions set by a resident population adopting a singular strategy η^{ss} , any mutant population of small size adopting a (nearby or not) strategy η^{inv} will be also in equilibrium, i.e., all mutant strategies perform equally well.*

3.2.1. Reproductive value at the singular strategy

According to the characterization of the equilibrium defined by the singular strategy and since the sum of the i th column of \mathbf{P} at the singular strategy is equal to $s_i^* + f_i^*$, it follows that $\mathbf{1}'\mathbf{P} = \mathbf{1}'$. So, the normalized vector of reproductive values $\tilde{\mathbf{u}}$ is equal to $\mathbf{1}$, which is equivalent to say that $r_{1i} = 1$ for all $1 \leq i \leq n$ (see Section 2). That is we again obtain the same conclusion as before: at the equilibrium imposed by the singular strategy, all the dominance classes have the same reproductive value which is equal to 1.

Another way to look at the neutrality among dominance classes is by rewriting (11) as

$$\frac{f_i^*}{1 - s_i^*} = 1, \quad i = 1, \dots, n, \tag{12}$$

which says that, at the equilibrium defined by a singular strategy η^{ss} , the expected life-time production of offspring of an individual that remains always in the same class is equal to 1 for any

class. In other words, there exists equality of fitness among all dominance classes, which is equal to the fitness corresponding to the optimal strategy given by η^{ss} . From a biological point of view, this explains the neutral evolutionary stability of the singular strategy: under the ESS conditions, all dominance classes are equally suitable for staying alive and reproduce.

Remarks. The neutrality of mutant strategies when the resident plays the singular strategy already obtained is completely analogous to the one obtained in [22] for evolutionarily stable dispersal strategies in the context of metapopulation theory when there is no cost of dispersal. In this case, the reproductive value of every local population (habitat patch) is the same when the evolutionary stable dispersal strategy is adopted in the whole metapopulation and gives rise to the so-called *ideal free distribution* among habitat patches (see [19]). In a different context, namely, the evolution of the timing of reproduction in a semelparous individuals, a neutrality result is also found in [24,25]. In particular, in [25] it is claimed that neutral singular strategies is what one should expect when a model contains more than one interaction variable, as in our case, and, so, that neutrality has to be used as ‘a guiding principle for the search of singular points’. In fact, this could be the key point for overcoming the apparent incompatibility between matrix games and (density-dependent) optimization models regarding the outcome of evolutionary processes that has been pointed out by some authors as, for instance, in [27] (see Section 6 for a discussion).

3.3. Spread of the (mutant) singular strategy and convergence stability

Let us now analyze by means of numerical simulations the conditions for the ability to spread as a mutant, of a singular strategy of the adaptive dynamics of the model. First of all, since we have already proved that, at the demographical equilibrium N^* determined by the singular strategy η^{ss} , $R_0(\eta, N^*(\eta^{ss})) = 1$ for all η , we are in the situation in which the ability to spread is equivalent to being convergence stable. Therefore, we only need to determine the conditions for the invading potential of the singular strategy to have also guaranteed its convergence stability.

More precisely, for the case of having three dominance classes ($n = 3$), we will see numerically under which conditions η^{ss} has the ability to spread as mutant under the following choices of $s_i(N)$ and $f_i(N)$, $i = 1, 2, 3$,

$$s_i(N) = s_i^0 \exp(-\gamma_i \phi_i(N)), \quad f_i(N) = f_i^0 \exp(-\gamma_i \phi_i(N)), \tag{13}$$

where, for each class, s_i^0 and f_i^0 satisfy hypothesis (H4), and $\gamma_i > 0$ denotes the sensitivity coefficient to competition (sometimes also called *competition coefficient*). Such a form is sometimes called *overcompensatory* relation (see [28] for other non-linearities in the vital rates). Moreover, we will consider the following weighted averages of the population distribution $\phi_i(N)$:

$$\begin{aligned} \phi_1(N) &= w_1 N_1 + \frac{1}{2}(1 - w_1)(N_2 + N_3), \quad 0 < w_1 \leq 1, \\ \phi_2(N) &= w_2 N_2 + (1 - w_2)N_3, \quad 0 < w_2 \leq 1, \\ \phi_3(N) &= (1 - w_3)N_2 + w_3 N_3, \quad 0 < w_3 \leq 1. \end{aligned}$$

According to (H5) in Section 2.2, \mathbf{W} has to be an invertible matrix and, hence, in this case this means that $\det(\mathbf{W}) = w_1(w_2 + w_3 - 1) \neq 0$. So, we assume $w_2 + w_3 \neq 1$ and $w_1 > 0$.

From this choice of the matrix $\mathbf{W} = (w_{ij})$ it could seem that we are restricting ourselves to a very particular case, namely, a case in which $\sum_j w_{ij} = 1$. However, it is easy to see that, in our case

as well as in many non-linearities appearing frequently in structured population models (see [28] for examples), this is not a restrictive assumption since the competition coefficient γ_i in the expressions of $s_i(N)$ and $f_i(N)$ allow us to consider $\phi_i(N)$ as normalized weighted sums, i.e., weighted averages of the population, without loss of generality. More precisely, if $\sum_j w_{ij} = w_i^0 > 0$, $i = 1, 2$, then we can write

$$\gamma_i \phi_i(N) = \gamma_i \sum_j w_{ij} N_j = \gamma_i w_i^0 \sum_j \frac{w_{ij}}{w_i^0} N_j = \tilde{\gamma}_i \sum_j \tilde{w}_{ij} N_j = \tilde{\gamma}_i \tilde{\phi}_i(N)$$

where $\sum_j \tilde{w}_{ij} = 1$ for all i . Note that, in this normalized case, the competition coefficient $\tilde{\gamma}_i$ has a nice biological interpretation since is proportional to the number of per capita aggressive interactions of an i -class individual per time period, w_i^0 .

On the other hand, in the previous choice of w_{ij} it is assumed a sort of hierarchy in the social structure since the weight of the subordinates in the weighted averages of the other classes is zero ($w_{21} = w_{31} = 0$), while all classes appear in $\phi_1(N)$. In terms of aggressive interactions, this choice assumes that the expected number of aggressive encounters in the subdominant and dominant classes is independent of the subordinates while the expected number of aggressive encounters suffered by the latter depends on the dominant and subdominant classes. Moreover, according to the description of the dominance hierarchy given in Section 2.2, if class 3 has to be the dominant one then $w_2 < w_3$. Finally, $w_1 > 0$ says that subordinates compete among themselves for the available resources ‘left’ by the dominant class.

Note that, under the choice of the survival rates and fecundities given by (13), and even though the model is non-linear, the equilibrium (N_1^*, N_2^*, N_3^*) determined by the singular strategy can be explicitly obtained because, from (11), it follows that N^* is the unique solution of the linear system

$$\begin{pmatrix} w_1 & (1 - w_1)/2 & (1 - w_1)/2 \\ 0 & w_2 & 1 - w_2 \\ 0 & 1 - w_3 & w_3 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix} = \begin{pmatrix} c_1 \\ c_2 \\ c_3 \end{pmatrix} \tag{14}$$

with c_i being positive constants given by

$$c_i = \frac{1}{\gamma_i} \ln(s_i^0 + f_i^0). \tag{15}$$

In particular, from this system it follows that survival probabilities and fecundities at this equilibrium are given by

$$s_i^* = \frac{s_i^0}{s_i^0 + f_i^0}, \quad f_i^* = \frac{f_i^0}{s_i^0 + f_i^0}, \quad i = 1, 2, 3.$$

Hence, the equilibrium is given by

$$\begin{aligned} N_1^* &= \frac{c_1 - \frac{1}{2}(1 - w_1)(N_2^* + N_3^*)}{w_1}, \\ N_2^* &= \frac{c_2 w_3 - c_3(1 - w_2)}{w_2 w_3 - (1 - w_2)(1 - w_3)}, \\ N_3^* &= \frac{c_3 w_2 - c_2(1 - w_3)}{w_2 w_3 - (1 - w_2)(1 - w_3)}, \end{aligned} \tag{16}$$

and it is well-defined since $w_1 > 0$ and $w_2 + w_3 \neq 1$ implies $w_2w_3 - (1 - w_2)(1 - w_3) \neq 0$ (in fact, $w_2 + w_3 < (>)1$ if and only if $w_2w_3 < (>)(1 - w_2)(1 - w_3)$).

At this point, it is important to realize three important facts. First, the assumption of a *dominance hierarchy* in the structure of the population and, so, to consider $\phi_1(N) \neq \phi_2(N) \neq \phi_3(N)$, is a *necessary condition* for the existence of a unique positive solution to (14). In other words, the existence of an optimal transition strategy essentially depends on the fact that (11) defines a unique equilibrium $N^* > 0$ and, under the present choice of s_i and f_i , this is only possible if each dominance class has its own environmental conditions. Otherwise, when the dimension of the environment (i.e. the number of interaction variables) is less than the number of dominance classes, it is not possible to find out a singular strategy according to our procedure because there exists a continuum of solutions to (14) and, hence, the hypothesis of the theorem about the existence of a globally stable equilibrium of the model is not fulfilled.

Secondly, the equilibrium N^* corresponding to the singular strategy η^{ss} is *independent* of the particular choice of the strategy vector η . In particular this means that, when the dimension of η is less than n , then the singular strategy is uniquely determined from (5) once N^* is replaced by (16). Otherwise, i.e. when the dimension of $\eta \geq n$, then there exists a continuum of strategies defining the same equilibrium N^* and, so, there does not exist a unique singular strategy but a (infinite) set of singular strategies defining the same environmental conditions $\{\phi_i\}$.

Thirdly, according to (16), it is possible to have a component of the equilibrium defined by a singular strategy equal to zero. However, the corresponding values of the (internal) singular strategy are non-admissible for some of its components (see, for instance, expressions (18) and (19) for η in the examples below when $N_2^* = 0$). The only possibility of having $N_2^* = 0$ (or $N_3^* = 0$) is that $\tau_{21} = \tau_{23} = 0$ (or $\tau_{31} = \tau_{32} = 0$) in \mathbf{T} , but this amounts to a reducible projection matrix and, so, (H3) is not fulfilled. Indeed, any strategy with these values lies on the boundary of the trait space and, hence, the fitness gradient needs not be zero at such a strategy.

On the other hand, in order to get some rough feeling about possible conditions for the spread of η^{ss} as a mutant strategy, notice that (N_2^*, N_3^*) is given by the intersection point of the straight lines defined by the second and third equation in (14). Clearly, their relative position in \mathbb{R}_+^2 is determined by the relationships among the parameters s_i^0, f_i^0 , and w_i ($i = 2, 3$) since, depending on them, the lines may or not may intersect in the interior of \mathbb{R}_+^2 . If they do, then for $N^* > 0$ it is required that

$$\frac{1 - w_2}{w_3} < (>) \frac{c_2}{c_3} < (>) \frac{w_2}{1 - w_3}, \quad \text{if } w_2 + w_3 > (<) 1. \tag{17}$$

Although the (ecological) stability of N^* is the same in both cases as the bifurcation from $(1, \mathbf{0})$ does not depend on the condition $w_2 + w_3 > 1$, it seems likely that the convergence stability of the singular strategy depends on satisfying or not this condition.

3.3.1. Two case studies

Having in mind that our final goal is to give an explanation of the observed bimodal distributions of badges of social status, we have concentrated our study on what we have called *the dilemma of the subdominants*. The idea is to consider the following *tridiagonal* transition matrix $\mathbf{T} = (\tau_{ij})$ of order 3

$$\begin{pmatrix} 1 - \tau_{21} & \tau_{12} & 0 \\ \tau_{21} & 1 - \tau_{12} - \tau_{32} & \tau_{23} \\ 0 & \tau_{32} & 1 - \tau_{23} \end{pmatrix}$$

and to focus our analysis on a strategy η having as components the transition probabilities of the second class, the subdominant class, to see which are their optimal values. Precisely, we will consider as evolutionary variable the vector $\eta = (\tau_{12}, \tau_{32})$. Notice that this is an admissible strategy since $\tau_{i2} \neq 0$ for $i = 1, 2, 3$. However, it is important to realize that the equilibrium N^* corresponding to a singular strategy η^{ss} is independent of the particular choice of η since N^* is obtained from condition (11) which does not depend on η . To illustrate other possibilities of evolutionary variables and due to its own importance, we also consider the standard size-structured model with the probabilities of growth defining the evolutionary variable, i.e., with $\eta = (\tau_{21}, \tau_{32})$.

For the case of the dilemma of the subdominants, it follows from the equilibrium equations with a projection matrix of order 3 that

$$\tau_{12}^{ss} = \frac{(1 - \tau_{11})s_1^*N_1^* - (1 - s_2^*)N_2^* - (1 - s_3^*)N_3^*}{s_2^*N_2^*}, \quad \tau_{32}^{ss} = \frac{(1 - \tau_{33}s_3^*)N_3^*}{s_2^*N_2^*}, \tag{18}$$

where τ_{11} and τ_{33} are fixed beforehand and $\tau_{22} = 1 - \tau_{12} - \tau_{32}$.

Similarly, for the standard size-structured model, it follows

$$\tau_{21}^{ss} = \frac{(1 - s_2^*)N_2^* + (1 - s_3^*)N_3^*}{s_1^*N_1^*}, \quad \tau_{32}^{ss} = \frac{(1 - s_3^*)N_3^*}{s_2^*N_2^*}, \tag{19}$$

since, in this case, $\tau_{12} = 0$ and $\tau_{33} = 1$.

3.3.2. Explanation of the simulations

Once the equilibrium distribution N_{ss}^* determined by the singular strategy is obtained from (16) for a given choice of the parameter values $(w_i, \gamma_i, s_i^0, f_i^0)$, the value itself of the singular strategy η^{ss} is computed, depending on the analyzed case, from (18) or from (19). Then it is computed, firstly, the equilibrium distribution N^* of a resident population adopting a strategy η^{res} different from η^{ss} , and, secondly, the value of R_0 of the η^{ss} -mutant in such a resident population (i.e., the dominant eigenvalue of $\mathbf{R}(\eta^{ss}, N^*(\eta^{res}))$). Although other forms for s_i and f_i have been also considered, no significant differences have been observed with respect to the results below.

A dominant eigenvalue R_0^{ss} of the next generation matrix $\mathbf{R}(\eta^{ss}, N^*(\eta^{res}))$ greater than 1 indicates an initial spread of the mutant adopting the singular strategy η^{ss} under the conditions set by the resident equilibrium population N^* adopting $\eta^{res} \neq \eta^{ss}$ (i.e., an initially successful invasion). Conversely, if $R_0^{ss} < 1$, the number of η^{ss} -mutants decreases and, hence, the strategy can not spread under such environmental conditions. Notice that use of R_0^{ss} as a measure of the success of an invasion is completely equivalent to use of the dominant eigenvalue of the projection matrix $\mathbf{P}(\eta^{ss}, N^*(\eta^{res}))$ under the hypotheses of the model (see [28], Theorem 1.1.3).

Figs. 2 and 3 show some results for the spread of mutants adopting the singular strategy η^{ss} defined by the transition probabilities τ_{12} and τ_{32} from the middle class (subdominant class), and with τ_{11} and τ_{33} being fixed. In this case, there is the restriction $\tau_{12} + \tau_{32} \leq 1$, the equality being fulfilled when $\tau_{22} = 0$. Figs. 4 and 5 show the corresponding results of the spread of η^{ss} -mutants for the standard size-structured model. In this case, $\eta = (\tau_{21}, \tau_{32})$. In all the simulations, $\gamma_i = 0.01$



Fig. 2. Spread of the singular strategy η^{ss} when $w_2 + w_3 > 1$ in the case of the *dilemma of the subdominants* with a tridiagonal transition matrix. The success of the spread (invasion) of η^{ss} is measured in terms of $R_0 = R_0(\eta^{ss}, N^*(\eta))$ with $\eta = (\tau_{12}, \tau_{32})$ and such that $\tau_{12} + \tau_{32} \leq 1$. Parameter values: $w = (0.3, 0.4, 0.8)$, $s^0 = (0.810, 0.775, 0.770)$, $f^0 = (0.39, 0.39, 0.39)$, $(\tau_{11}, \tau_{33}) = (0.3, 0.9)$, $\eta^{ss} = (0.113557, 0.526599)$. The circles in the plot correspond to numerical outputs of the simulations with: (a) $\eta = (\tau_{12}, \eta_2^{ss})$, and (b) $\eta = (\eta_1^{ss}, \tau_{32})$. In both cases, $R_0 > 1$ for $\eta \neq \eta^{ss}$.

and the parameters of the vital rates are specified. All the numerical experiments follow one-dimensional paths in a two dimensional η -space. Along these paths, one of the components of the (resident) strategy η_i^{res} ($i = 1, 2$) remains constant and is equal to the corresponding one of the singular strategy η_i^{ss} .

As it can be immediately seen, the sign of $w_2 + w_3 - 1$ or, equivalently, the sign of $w_2 w_3 - (1 - w_2)(1 - w_3)$, is the factor that determines the success of the spread of η^{ss} -mutants when they

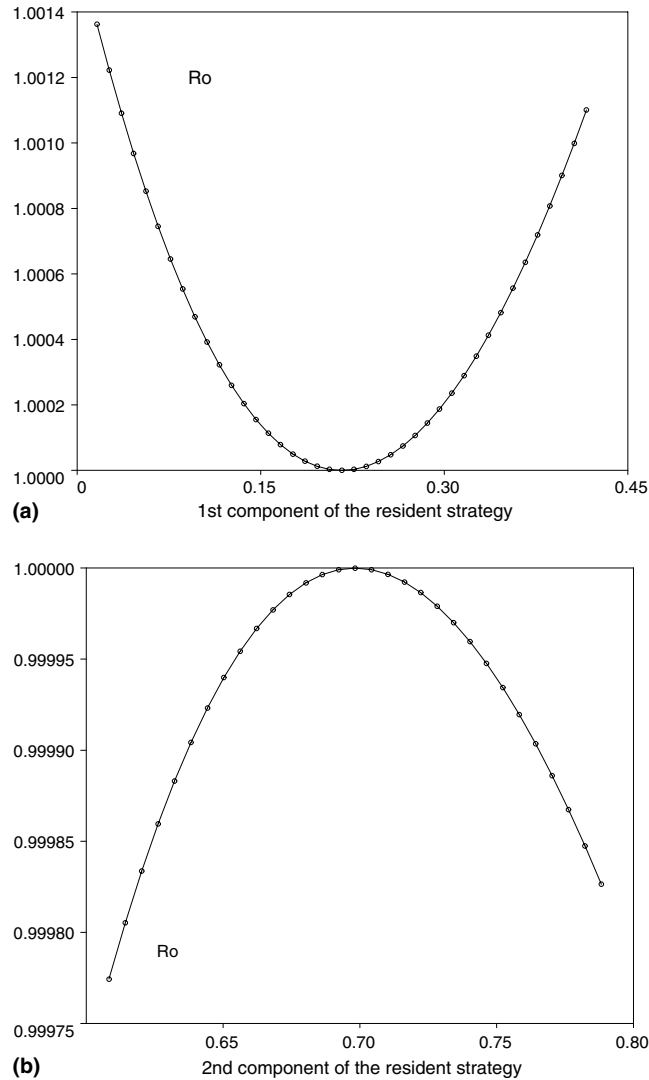


Fig. 3. Spread of the singular strategy η^{ss} when $w_2 + w_3 < 1$ in the case of the *dilemma of the subdominants* with a tridiagonal transition matrix. The success of the spread (invasion) of η^{ss} is measured in terms of $R_0 = R_0(\eta^{ss}, N^*(\eta))$ with $\eta = (\tau_{12}, \tau_{32})$ and such that $\tau_{12} + \tau_{32} \leq 1$. Parameter values: $w = (0.3, 0.4, 0.4)$, $s^0 = (0.810, 0.775, 0.770)$, $f^0 = (0.39, 0.39, 0.39)$, $(\tau_{11}, \tau_{33}) = (0.3, 0.9)$, $\eta^{ss} = (0.216192, 0.698261)$. The circles in the plot correspond to numerical outputs of the simulations with: (a) $\eta = (\tau_{12}, \eta_2^{ss})$ (where $R_0 > 1$), and (b) $\eta = (\eta_1^{ss}, \tau_{32})$ (where $R_0 < 1$).

appear in a resident population at equilibrium adopting $\eta \neq \eta^{ss}$. From Figs. 2 and 4, it follows that, as far as $w_2 + w_3 > 1$ (or $w_2 w_3 > (1 - w_2)(1 - w_3)$), η^{ss} -mutants spread in resident populations playing another (nearby or not) strategy. In contrast, when $w_2 + w_3 < 1$, there are always nearby strategies to the singular strategy that can not be invaded (when adopted by the resident) by any η^{ss} -mutant (see Figs. 3 and 5). More precisely, when $w_2 + w_3 < 1$, the mapping $\eta \rightarrow R_0(\eta^{ss}, N^*(\eta))$ has a saddle point at the singular strategy η^{ss} , which means that the second

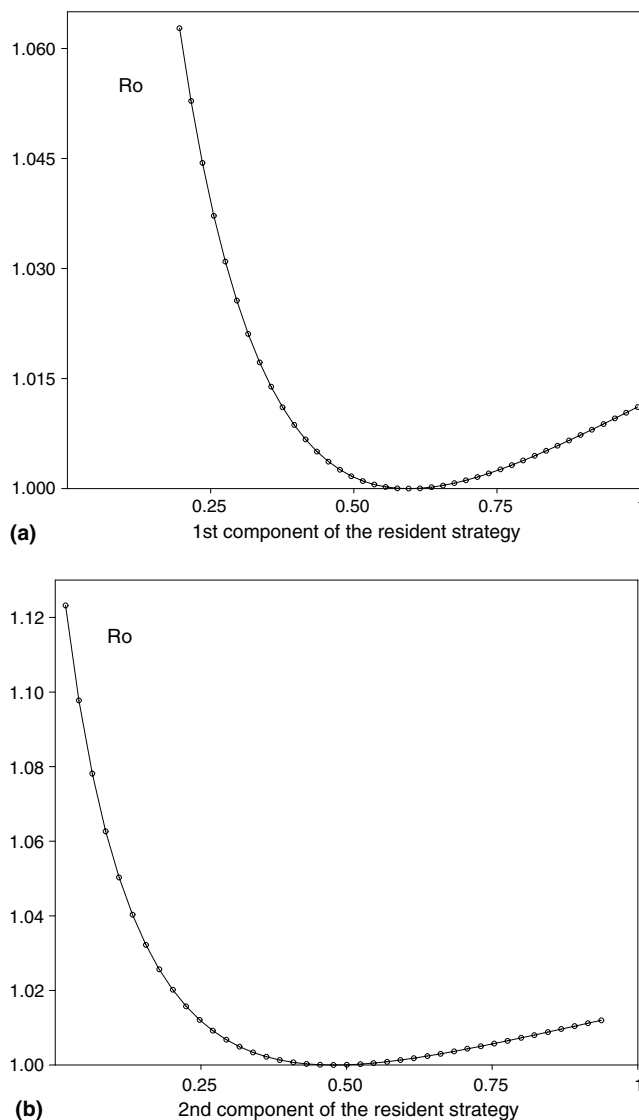


Fig. 4. Spread of the singular strategy η^{ss} when $w_2 + w_3 > 1$ in a *standard size-structured model*. The success of the spread (invasion) of η^{ss} is measured in terms of $R_0 = R_0(\eta^{ss}, N^*(\eta))$ with $\eta = (\tau_{21}, \tau_{32})$. Parameter values: $w = (0.3, 0.6, 0.9)$, $s^0 = (0.810, 0.775, 0.770)$, $f^0 = (0.39, 0.39, 0.39)$, $\eta^{ss} = (0.595688, 0.477555)$. The circles in the plot correspond to numerical outputs of the simulations with: (a) $\eta = (\tau_{21}, \eta_2^{ss})$, and (b) $\eta = (\eta_1^{ss}, \tau_{32})$. In both cases, $R_0 > 1$ for $\eta \neq \eta^{ss}$.

matrix in (6) has (two) real eigenvalues of opposite signs. This implies that there is some symmetric, positive definite covariance matrix for which the singular strategy is an unstable equilibrium of the corresponding canonical equation of the AD (see [34] for details).

The difference $w_2 w_3 - (1 - w_2)(1 - w_3)$ is a measure of the balance of an average of competition effects within $(w_2 w_3)$ and between $((1 - w_2)(1 - w_3))$ intermediate and dominant classes, and its

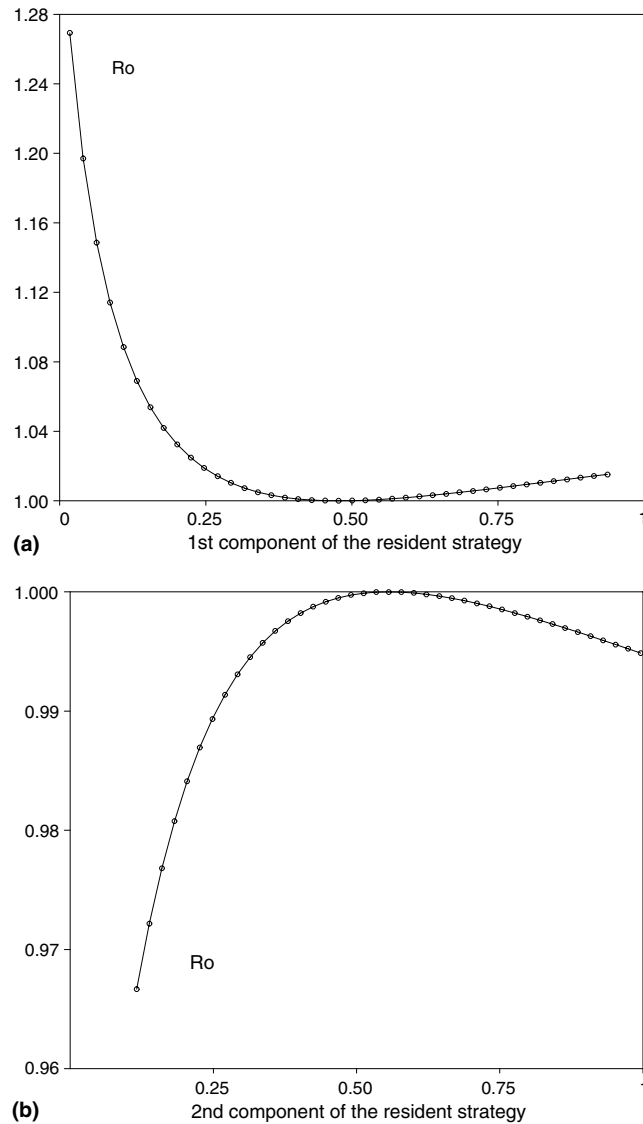


Fig. 5. Spread of the singular strategy η^{ss} when $w_2 + w_3 < 1$ in a *standard size-structured model*. The success of the spread (invasion) of η^{ss} is measured in terms of $R_0 = R_0(\eta^{ss}, N^*(\eta))$ with $\eta = (\tau_{21}, \tau_{32})$. Parameter values: $w = (0.2, 0.3, 0.4)$, $s^0 = (0.810, 0.775, 0.770)$, $f^0 = (0.39, 0.39, 0.39)$, $\eta^{ss} = (0.477187, 0.556177)$. The circles in the plot correspond to numerical outputs of the simulations with: (a) $\eta = (\tau_{21}, \eta_2^{ss})$ (where $R_0 > 1$), and (b) $\eta = (\eta_1^{ss}, \tau_{32})$ (where $R_0 < 1$).

sign determines the success of the initial spread of singular strategy. Notice that such a difference, which appears in the expression of the η^{ss} -equilibrium, is assumed to be non-zero to guarantee that the matrix $\mathbf{W} = (w_{ij})$ is invertible.

In summary, only when *the average competition within groups is bigger than the average competition between groups for the dominant and intermediate classes*, i.e. when $w_2 w_3 >$

$(1 - w_2)(1 - w_3)$, a singular strategy has the ability to spread in any resident population adopting a different (nearby or not) strategy and, hence, is convergence stable for any covariance matrix due to its neutral evolutionary stability. Note that, in terms of the classical definition of ESS [19], neutral evolutionary stability plus invading potential implies that a singular strategy is, in fact, a (classical) ESS. Therefore, from now on, we denote ESS such a singular strategy.

In terms of animal behaviour, the conclusion is that the presence of a *like-versus-like* aggression within dominant and subdominant (or intermediate) classes is a sufficient condition for the convergence stability of the singular strategy.

4. Evolutionary stability of bimodality

One aspect of the model that concerns us is the shape of a non-trivial equilibrium distribution of sizes of badges and its relation with the dominance role of the plumage trait (colour patch(es)). More precisely, from the field observations (see Introduction), it follows that a bimodal distribution with respect to a given colour patch has to be an output of the model – under some suitable choices of the parameter values – when this colour patch is only related to dominance status. Conversely, when the colour patch has also a sexual role, the equilibrium distribution becomes unimodal with its maximum in the middle classes. Our aim is to propose an explanation of how to pass from one situation to the other by means of changes in the values of suitable parameters of the model and, moreover, to give a biological interpretation of these changes. Therefore, let us turn our interest towards the shape of the equilibrium of a population adopting an ESS and see when bimodality is evolutionary feasible or, in other words, under which conditions bimodality can be observed in nature according to the present model.

Assuming, as in the previous section, that survival probabilities and fecundities are given by (13) for $i = 1, \dots, n$, the equilibrium N^* determined by the ESS satisfies the linear system $\mathbf{W}N^* = C$ with $C = (c_1, \dots, c_n)'$ and c_i given by (15). So, an explicit expression of N^* is easily obtained although the model is non-linear. This fact allows us to establish analytical conditions on the parameters s_i^0, f_i^0 and w_i^0 for N^* to be *positive* and *bimodal*. In particular, bimodality will be obtained whenever $N_i^* > N_{i+1}^*$ in low ranked classes (subordinate classes) while $N_i^* < N_{i+1}^*$ in high ranked classes (dominant classes). If the maxima of the equilibrium are in both extremes of the class distribution, then it is obviously required that $N_1^* > N_2^*$ and $N_{n-1}^* < N_n^*$.

4.1. Bimodality in models with n -dominance classes

In order to get an insight into the features of bimodality in terms of the parameters of the model, let us start with the simplest matrix \mathbf{W} satisfying the hypothesis of like-versus-like aggression which guarantees the convergence stability of the singular strategy. Clearly, such a matrix is the diagonal matrix $\mathbf{W} = \text{diag}(w_1, \dots, w_n)$ with $w_i > 0$ for all i . In this case, the ESS equilibrium is simply given by $N_i^* = c_i/w_i$ for $i = 1, \dots, n$. That is, the abundance of the i -class at the ESS equilibrium increases with its potential survival probability (s_i^0) and fecundity (f_i^0), and decreases with its aggression rate (w_i). Therefore, as long as $s_i^0 + f_i^0$ are similar for all dominance class, those that are more aggressive (usually the dominant classes) will have higher values of w_i and, hence, a lower number of individuals at equilibrium, with respect to those that are less

aggressive. On the contrary, high enough values of $s_i^0 + f_i^0$ can compensate the aggressions in dominant classes, whereas low aggression rates allow for increasing the number of individuals of subordinate classes although their inherent survival and fecundities are lower than those of the dominant classes. Consequently, when such a balance among different components of the life history occurs, it may result in bimodal ESS equilibria.

In the previous choice of \mathbf{W} , the simplest one, all classes are uncoupled. In particular, there is no dominance (or ranking) hierarchy between classes. So, let us consider the simplest matrix \mathbf{W} reflecting a dominance hierarchy between any pair of consecutive classes, namely,

$$\mathbf{W} = \begin{pmatrix} w_1 & 1 - w_1 & 0 & 0 & \dots & 0 \\ 0 & w_2 & 1 - w_2 & 0 & \ddots & 0 \\ 0 & 0 & \ddots & \ddots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \ddots & 0 \\ 0 & 0 & \dots & 0 & w_{n-1} & 1 - w_{n-1} \\ 0 & 0 & \dots & 0 & 0 & 1 \end{pmatrix},$$

with $0 \leq w_{ij} \leq 1$ and where, to reduce the number of involved parameters and without loss of generality, it is assumed that $w_{ii} + w_{i,i+1} = 1$ for all i .

This choice of \mathbf{W} is a sort of generalization of the hypothesis of like-versus-like aggression in which class $i + 1$ is dominant to class i as $w_{i,i+1} = 1 - w_i > w_{i+1,i} = 0$. Again, the expression of N^* is easily obtained and it is given by

$$N_i^* = \frac{c_i}{w_i} + \sum_{j=i+1}^n (-1)^{i+j} \left(\prod_{k=i}^{j-1} \frac{1 - w_k}{w_k} \right) \frac{c_j}{w_j}, \quad i = 1, \dots, n - 1,$$

and $N_n^* = c_n$, where $w_n := 1$ in the expression of N_i^* for convenience of notation. Note that, if one assumes $w_i > 1/2$ for all i to impose within-class aggressions to be more frequent than between-class aggressions, the product in the second term tends to zero as the number of factors increases since $(1 - w_k)/w_k < 1$ for all k . The latter means that the contribution of high ranked (or dominant) classes to the equilibrium values of low ranked (or subordinate) classes tends to be negligible as the number of dominance classes increases.

Using the previous expression of N_i^* , the condition $N_i^* > N_{i+1}^*$ (for low ranked classes) amounts to

$$c_i > \frac{c_{i+1}}{w_{i+1}} + \sum_{j=i+2}^n (-1)^{i+j+1} \left(\prod_{k=i+1}^{j-1} \frac{1 - w_k}{w_k} \right) \frac{c_j}{w_j}, \quad i = 1, \dots, n - 2, \tag{20}$$

which is equivalent to $c_i > N_{i+1}^*$. This result is in agreement with what we already knew about c_i because the latter is a convex linear combination of N_i^* and N_{i+1}^* and, so, $N_{i+1}^* \leq c_i \leq N_i^*$ for all $w_i \in [0, 1]$ under the hypothesis $N_i^* > N_{i+1}^*$.

Note that, from the condition $N_i^* > 0 \forall i$, it follows that the second term of the RHS of (20) is non-positive for all $w_i \in [0, 1]$. So, a *sufficient* condition for $N_i^* > N_{i+1}^*$ (in low ranked classes) is

$$c_i > \frac{c_{i+1}}{w_{i+1}}.$$

Similarly, the condition $N_i^* < N_{i+1}^*$ for high ranked classes is equivalent to $c_i < N_{i+1}^*$, the opposite inequality to (20). That is,

$$c_i + \sum_{j=i+2}^n (-1)^{i+j} \left(\prod_{k=i+1}^{j-1} \frac{1-w_k}{w_k} \right) \frac{c_j}{w_j} < \frac{c_{i+1}}{w_{i+1}}, \quad i = 1, \dots, n-2.$$

As before, it was known beforehand that $N_i^* \leq c_i \leq N_{i+1}^*$ for all $w_i \in [0, 1]$ if one assumes $N_i^* < N_{i+1}^*$. For the two highest ranked classes, $N_{n-1}^* < N_n^*$ is equivalent to

$$c_{n-1} < c_n.$$

Therefore, in order to get bimodal equilibria it is enough (but not necessary) for subordinate classes that each class has a potential fitness (measured by c_i) greater than that of the next ranked class times the factor $1/w_{i+1}$ which is bigger than 1. In particular, this means that the difference of potential fitnesses between class i and class $i + 1$ required for bimodality can be relaxed by raising w_{i+1} , the aggression rate of class $i + 1$. On the other hand, in dominant classes, this relationship between potential fitnesses is just the converse one. More precisely, a necessary and sufficient condition is to have an increase of the ratio of potential fitness to aggression rate enough to compensate the potential fitness of the previous class plus an average of ratios of potential fitness to aggression rate (c_j/w_j) for all higher ranked classes.

Less simple $n \times n$ matrices \mathbf{W} may be considered to obtain the corresponding conditions for bimodality as, for instance, *upper triangular matrices* with $\sum_j w_{ij} = 1$ for all i . The environmental variable of i -class, $\phi_i(N)$, under these matrices is determined by all the higher ranked classes in addition to itself. In this particular case, it is easily seen along the same lines as before that the same sufficient conditions for bimodality as in the previous choice of \mathbf{W} still hold. Note that, also in this case, c_i are convex linear combinations of N_j with $j \geq i$, and that the corresponding expression of N_i^* is also given by a first positive term (c_i/w_{ii}) plus a second term which is negative under the hypothesis $N_i^* > 0$ for all i .

In general, however, more general $n \times n$ \mathbf{W} matrices give rise to complicated (although explicit) expressions for the equilibrium N^* which make cumbersome (if not impossible) to arrive at simple and illustrative conditions for bimodality. So, let us return to the examples considered in the previous section with a matrix \mathbf{W} that is not an upper triangular matrix and which are more closely related to the field observations.

4.2. Bimodality in the two case studies

First of all note that, from the expression of the equilibrium at the ESS given by (16) and assuming $w_2 + w_3 > 1$, $N^* > 0$ implies the following conditions on the parameter values of the model

$$N_1^* > 0 \iff c_1 > (1 - w_1) \frac{c_2(2w_3 - 1) + c_3(2w_2 - 1)}{2(w_2 + w_3 - 1)}, \tag{21}$$

$$N_2^* > 0 \iff \frac{c_2}{c_3} > \frac{1 - w_2}{w_3}, \tag{22}$$

$$N_3^* > 0 \iff \frac{c_3}{c_2} > \frac{1 - w_3}{w_2}. \tag{23}$$

In particular, (22) and (23) imply that the RHS of (21) is non-negative and is equal to 0 only when $w_1 = 1$.

Imposing the first condition for having a bimodal ESS equilibrium distribution, namely, $N_2^* < N_3^*$, it follows

$$N_2^* - N_3^* = \frac{c_2 - c_3}{w_2 + w_3 - 1} < 0,$$

and, assuming the ESS-condition $w_2 + w_3 > 1$, the inequality amounts to

$$c_2 < c_3$$

where c_i , given by (15), involves all the components of the fitness in our model, namely, the inherent capabilities of the i -class to survive (s_i^0) and reproduce (f_i^0), and the competition coefficient (γ_i).

In particular, if one assumes the same competition coefficient for all (bib-size) classes, i.e., $\gamma_i = \gamma > 0$ for all i , then $c_2 < c_3$ is equivalent to $s_2^0 + f_2^0 < s_3^0 + f_3^0$. This implies that *for an ESS-bimodality it is needed that the sum of the maximum probability values of survival and reproduction (i.e., potential fitness) for the dominant class is greater than the corresponding sum for the intermediate class.*

The second condition for having a bimodal ESS equilibrium distribution, $N_1^* > N_2^*$, implies $2c_1 > N_2^* + N_3^* - w_1(N_3^* - N_2^*)$. Again, assuming $w_2 + w_3 > 1$, this condition is equivalent to

$$c_1 > \frac{c_2(2w_3 - 1) + c_3(2w_2 - 1) - (c_3 - c_2)w_1}{2(w_2 + w_3 - 1)}. \tag{24}$$

Note that, under the assumption $c_2 < c_3$,

$$\frac{c_2(2w_3 - 1) + c_3(2w_2 - 1) - (c_3 - c_2)w_1}{2(w_2 + w_3 - 1)} < c_3 - \frac{(c_3 - c_2)w_1}{2(w_2 + w_3 - 1)} < c_3,$$

and, so, the minimum value of c_1 required for having bimodal ESS-equilibria is always less than c_3 for any $0 < w_1 \leq 1$ whenever $c_2 < c_3$ and $w_2 + w_3 > 1$. On the other hand, since condition (24) and the positivity condition (21) are almost equivalent for (very) small values of w_1 , an ESS-equilibrium N^* will be bimodal for a (very) wide range of those values of c_1 that guarantee $N_1^* > 0$.

In conclusion, *as far as the parameter values of the model verify $c_2 < c_3$ and (24) with c_i given by (15), any ESS equilibrium $N^* > 0$ of (4) corresponds to a bimodal distribution of dominance classes.*

Under the assumption $\gamma_i = \gamma$ for all classes, and if the inherent fecundity in the dominant class is equal to the one in the subdominant class, i.e., $f_3^0 = f_2^0$, equilibrium bimodality can not occur unless an increment of the inherent survival probability in the dominant class (s_3^0) takes place. On the other hand, recalling that γ_i is proportional to the number of per capita aggressive interactions of an i -class individual per time period ($w_i^0 = \sum_j w_{ij}$) when working with normalized $\phi_i(N)$, it follows that values of w_3^0 lower than values of w_2^0 can compensate lower survival probabilities and lead to bimodal equilibria. In other words, another way of obtaining bimodality comes from the assumption of different competition coefficients among dominance classes. In particular, if the

sum $s_i^0 + f_i^0$ is similar for all classes, a necessary condition for bimodality is that the competition coefficient in the dominant class (γ_3) is small enough compared with that of the subdominant class (γ_2). However, this last possibility seems not to be the case in the Siskin due to the high number of aggressions between individuals of the dominant class.

5. An example: the tridiagonal transition matrix

The decompose of the projection matrix as $\mathbf{T}_0 + \mathbf{F}$ is actually the case for most of life cycles and, of course, it is also our case. However, while the general expression for R_0 is well-known for discrete size-structured population models with one offspring class [28], its explicit expression and interpretation are not so well-known when reverse transitions are allowed. The main reason could be that, in standard size-structured models, only transitions from the i -class to the $(i + 1)$ -class are considered because shrinking is not usually considered. In our case, since we are concerned about transitions among dominance classes, it would be convenient to have an expression of R_0 that includes reverse transitions to model properly the dynamics of a rank-structured population.

The case where only one-step transitions (per time interval) are allowed is the simplest one with reverse transitions. The corresponding transition matrix is *tridiagonal* and it extends the examples we have previously considered in Section 3 to n dominance classes.

Note that, from the definition of \mathbf{R} , it follows that $\mathbf{R}(\mathbf{I} - \mathbf{T}_0) = \mathbf{F}$ which allows us to obtain an expression for the elements r_{1j} and, in particular, for R_0 since $R_0 = r_{11}$ (recall that only the first row \mathbf{R} is non-zero if there is only one class of newborns). Here we will obtain an expression of R_0 when one-step transition are allowed, i.e., for a tridiagonal transition matrix.

5.1. Explicit computation of R_0

Let us assume that the transition matrix \mathbf{T}_0 is tridiagonal, i.e., only transitions to adjacent classes are allowed. Then $(\mathbf{I} - \mathbf{T}_0)$ is also tridiagonal and the following recurrence among the elements r_{1j} of the matrix \mathbf{R} holds:

$$\frac{f_k}{1 - t_{kk}} = r_{1k} - r_{1,k-1} \frac{t_{k-1,k}}{1 - t_{kk}} - r_{1,k+1} \frac{t_{k+1,k}}{1 - t_{kk}}, \quad 1 \leq k \leq n, \tag{25}$$

where, for convenience of notation, $r_{10} = r_{1,n+1} := 0$. This expression says that the expected offspring *per* visit at stage k of an individual is equal to the expected offspring of an individual starting life in the class k minus two terms: the expected offspring of an individual starting life in the previous class times the probability of the (reverse) transition to this class from class k , and the expected offspring of an individual starting life in the next class times the probability of the transition to this class from class k .

Now, solving (25) for an arbitrary number n of classes and since $R_0 = r_{11}$, it follows

$$R_0 = \sum_{i=1}^n f_i \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j}, \tag{26}$$

where $t_{10} := 1$ and p_k satisfies the recurrence

$$p_{k-1} = \frac{t_{k-1,k}}{1 - t_{kk}} \frac{t_{k,k-1}}{1 - t_{k-1,k-1}} \frac{1}{1 - p_k}, \quad k = n, n - 1, \dots, 2, \tag{27}$$

with $p_n := 0$ and $p_k \in [0, 1)$ for $k = 1, \dots, n - 1$. Notice that, if reverse transitions are not allowed ($t_{i,i+1} = 0$, $1 \leq i \leq n - 1$), then $p_k = 0$ for all k and it immediately follows the well-known expression of R_0 for standard size-structured population models.

For instance, in case of having three dominance classes ($n = 3$), which is the one we have considered in the numerical simulations in Section 3, it follows that the net reproductive number is given by

$$R_0 = \frac{\frac{f_1}{1-t_{11}} + \left(1 - \frac{t_{32}}{1-t_{22}} \frac{t_{23}}{1-t_{33}}\right)^{-1} \left[\frac{t_{21}}{1-t_{11}} \frac{f_2}{1-t_{22}} + \frac{t_{21}}{1-t_{11}} \frac{t_{32}}{1-t_{22}} \frac{f_3}{1-t_{33}} \right]}{1 - \left(1 - \frac{t_{32}}{1-t_{22}} \frac{t_{23}}{1-t_{33}}\right)^{-1} \frac{t_{21}}{1-t_{11}} \frac{t_{12}}{1-t_{22}}},$$

where $1/(1 - t_{ii}) = \sum_{n=0}^{\infty} t_{ii}^n$ is the expected number of time steps in class i per visit, $(1 - \frac{t_{32}}{1-t_{22}} \frac{t_{23}}{1-t_{33}})^{-1}$ is equal to 1 plus the expected number of visits to class 2 from class 3, and, finally, $(1 - (1 - \frac{t_{32}}{1-t_{22}} \frac{t_{23}}{1-t_{33}})^{-1} \frac{t_{21}}{1-t_{11}} \frac{t_{12}}{1-t_{22}})^{-1}$ is the expected number of visits to the class 1 during the lifetime. In particular, note that in case that $t_{12} = 0$, the last expected number is equal to one since it is not possible to return to stage 1 from any other stage.

5.2. Neutral evolutionary stability of the ESS

Now, let us see in a straightforward manner the neutral stability of the ESS when \mathbf{T} is a $n \times n$ tridiagonal matrix, i.e., that $R_0(\eta, N^*(\eta^{ss})) = 1$ for all admissible η . First let us write R_0 given by (26) as

$$R_0 = \sum_{i=1}^{n-2} f_i \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} + \prod_{j=1}^{n-1} \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} \left(f_{n-1} + f_n \frac{t_{n,n-1}}{1 - t_{nn}} \right).$$

At the equilibrium determined by the singular strategy η^{ss} , $N^*(\eta^{ss})$, we have that $f_i^* = 1 - s_i^* \forall i$. So, since $s_n = t_{nn} + t_{n-1,n}$ and $s_j = t_{j,j} + t_{j-1,j} + t_{j+1,j}$ ($2 \leq j \leq n - 1$), it follows, using the recurrence (27), that the net reproductive number R_0 of any mutant population with $\eta \neq \eta^{ss}$ at $N^*(\eta^{ss})$ is given by

$$\begin{aligned} R_0(\eta, N^*(\eta^{ss})) &= \sum_{i=1}^{n-2} f_i^* \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} + \prod_{j=1}^{n-2} \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} \frac{t_{n-1,n-2}}{1 - p_{n-1}} \left(1 - p_{n-1} - \frac{t_{n-2,n-1}}{1 - t_{n-1,n-1}} \right) \\ &= \sum_{i=1}^{n-3} f_i^* \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} + \prod_{j=1}^{n-2} \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} \left[f_{n-2}^* + t_{n-1,n-2} \left(1 - \frac{t_{n-2,n-1}}{1 - t_{n-1,n-1}} \frac{1}{1 - p_{n-1}} \right) \right] \\ &= \sum_{i=1}^{n-3} f_i^* \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} + \prod_{j=1}^{n-3} \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} \frac{t_{n-2,n-3}}{1 - p_{n-2}} \left(1 - p_{n-2} - \frac{t_{n-3,n-2}}{1 - t_{n-2,n-2}} \right) \\ &= \sum_{i=1}^{n-4} f_i^* \prod_{j=1}^i \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} + \prod_{j=1}^{n-3} \frac{t_{j,j-1}}{1 - t_{jj}} \frac{1}{1 - p_j} \left[f_{n-3}^* + t_{n-2,n-3} \left(1 - \frac{t_{n-3,n-2}}{1 - t_{n-2,n-2}} \frac{1}{1 - p_{n-2}} \right) \right]. \end{aligned}$$

Repeating the same arrangements as before for the rest of the terms of the sum until the first one, it follows that the net reproductive number of a mutant adopting any strategy η when the resident population adopts the singular strategy η^{ss} and is in ecological equilibrium is

$$\begin{aligned}
 R_0(\eta, N^*(\eta^{ss})) &= \frac{t_{10}}{1-t_{11}} \frac{1}{1-p_1} \left[f_1^* + t_{21} \left(1 - \frac{t_{12}}{1-t_{22}} \frac{1}{1-p_2} \right) \right] \\
 &= \frac{1}{1-p_1} \left(1 - \frac{t_{12}}{1-t_{22}} \frac{t_{21}}{1-t_{11}} \frac{1}{1-p_2} \right) = 1,
 \end{aligned}$$

where, for convenience of notation, $t_{10} := 1$, and it is used that $s_1 = t_{11} + t_{21}$.

Remark. As the previous computation does not depend on the values of τ_{ij} appearing in the expression of R_0 , it also proves that $R_0(\eta, \mathbf{0}) = 1$ when $s_i^0 + f_i^0 = 1$, i.e., it proves that this condition on parameters s_i^0 and f_i^0 actually defines a bifurcation point from the extinction equilibrium $N^* = \mathbf{0}$ when the transition matrix is tridiagonal (see Section 2).

6. Concluding remarks & biological implications

In this paper we have considered a stage-structured model with a general transition matrix and no cost when moving among classes. The species we have in mind as a model species is the Siskin (*C. spinus*). Since males of this species display a plumage trait such that its size has been shown to act as a reliable badge of status, such individuals are categorized into (discrete) dominance classes according to it. On the other hand, the motivation of considering a general transition matrix is due to observed transitions to lower ranks occurring in individuals remaining in captivity under poor nutritional conditions (JCS, personal observation).

As evolutionary trait, we have considered a set of probabilities of moving among classes and, to assess invasibility, we use R_0 , the net reproductive number. From an evolutionary point of view, the first result we have obtained is that evolutionarily singular values of this trait determine demographic equilibria where *the reproductive value of all classes is the same and equal to one* (see Eq. (11)). This situation implies our second main result: the *neutral evolutionary stability* of the singular strategy. This means that, when a singular strategy is adopted by the resident, any small population of mutants with a (nearby or not) different strategy is also in equilibrium. Both results are, in fact, analogous to the one obtained in [22] for evolutionarily stable dispersal rates in metapopulations under the assumption of no cost of dispersal, and to those obtained in [24,25] for the evolutionarily stable timing of reproduction in semelparous organisms.

One can look at the neutrality result obtained in this paper, as well as in other papers as the previously cited, from the point of view of the evolutionary game theory and merely in terms of animal behaviour. In this case, a mixed strategy is a specification of the probabilities of the actions that an individual can do in any situation in which it may find itself [19]. So, any interior strategy vector η is a mixed strategy because, given the current class of an individual, it gives the probabilities of moving to any other class in the next period of time. In turn, pure strategies are of the form ‘when being in class i , move to class k (with probability one)’ and, therefore, they lie at the boundary of the trait space.

In the context of evolutionary matrix games, the process of substitution of strategies often leads to mixed ESSs and, as a consequence of the theorem of Bishop and Cannings, each pure strategy in the support of the mixed ESS, as well as any mixed strategy different from the ESS but containing pure strategies also in its support, must have the same fitness as the mixed ESS itself [19,27]. In other words, fitness equality of all strategies contained in a mixed ESS, once the latter is established in the population, is the prediction resulting from matrix games as a result of an evolutionary process. As it is pointed out in [27], such a prediction seems to be ‘qualitatively incompatible’ with that of optimization models, namely, that under evolutionary equilibrium conditions the strategy widespread in a natural population should have a higher fitness than any mutant strategy that could be present in the population.

However, the previous incompatibility is only apparent. Neutrality or fitness equality among different actions as the output of an evolutionary process has been also predicted, in the context of density-dependent optimization models, by means of the well-known concept of ‘ideal free distribution’ in metapopulation theory (see [19,22]) or, more recently, by the so-called ‘principle of indifference’ in [25] (or condition (12) in the present paper). The first essential feature of all these optimization models leading to neutral ESSs is that the dimension of the environment, i.e., the number interaction variables considered to introduce non-linearities in the dynamics, exceeds one. For instance, in metapopulation models, usually each local population experiences its particular environmental conditions and, in hierarchical models as the one we present in this paper, there are as many interaction variables as classes in the dominance hierarchy. The second essential feature is that, under the assumptions of most of these models, there does not exist a direct cost of a given action (for instance, to move to another patch in a metapopulation model) or, at least, the cost is always the same regardless of the action. Otherwise, neutrality may not be the output of the evolutionary process even though high dimensional environments are considered (see, for instance, [21] for a size-dependent model with a cost in the growth and a non-neutral ESS). Even if there is a cost associated to an action (for instance, to migrate to a given patch) but this cost is the same for any individual, neutrality arises again as a result of adaptation because, indeed, such a neutrality was already implicit in the assumption of a constant cost (see [23] for an example of an ideal free distribution in a metapopulation model with a cost of dispersal which is the same for any immigrant and only depends on the patch where an organism settles down – and not on the patch from which it comes from).

On the other hand, when (11) holds and the strategy vector η is defined by more than $n - 1$ probabilities, then there exists an infinite set of strategies satisfying the condition of singular strategy. To see that note that, when the n equations given by (11) hold, it is always possible to express one of the n equations of the model in terms of the other $n - 1$ equations. Therefore, there are $2n - 1$ linearly independent equations for n components of the equilibrium N^* plus the components of the vector η . In other words, we do not have to expect that the condition for a strategy to be singular defines a unique strategy when the evolutionary trait has more than $n - 1$ components. In any case, however, environmental conditions determined by any of the singular strategies will be the same as long as (11) defines a unique demographic equilibrium.

Under our choice of the vital rates and assuming a dominance hierarchy among members of the population belonging to different classes, such an equilibrium is, certainly, unique and it is obtained from the linear system of equations resulting from (11), which does not depend explicitly on τ . Numerically, when three dominance classes are considered, it follows our third main result,

namely, that any singular strategy turns out to be able to spread as invading strategy only when *the average competition within the dominant classes is bigger than the average competition between dominant classes*. This invading potential of the singular strategy in addition to its neutral evolutionary stability implies that the singular strategy is convergence stable. We conjecture that this is a general fact for this sort of hierarchical models which does not depend on the dimension of the trait space. This is, indeed, a generalization of what was conjectured in [21] for the particular case of size-dependent matrix models.

Therefore, measuring competition effects in terms of aggressive interactions and considering three dominance classes, to attain ESS we necessarily need intra-class aggression to be higher than inter-class one, especially in relation to dominant and subordinate classes (i.e., $w_2 w_3 > [1 - w_2][1 - w_3]$). Subordinates, in turn, have to be engaged in some intra-class aggression ($w_1 > 0$) but not too much necessarily. That is equivalent to say that the condition for hierarchical systems as the one assumed in this paper to be evolutionary stable is *like-versus-like aggression* between dominant individuals.

Like-versus-like aggression has been described for several species [2], including the Siskin [35], but not in others, where aggression mainly takes place from dominant to subordinate individuals (i.e., despotic aggression) [2,9]. Inter-specific differences may be explained by differences in social behaviour patterns between species [36]. However, we have to point out that most of the examples of despotic aggression so far described refer to species where plumage coloration is highly age or sex dependent [8,9,37], and this should not be regarded as true status signalling [2]. This is why we stated age independence as one of the assumptions for our approach, hypothesis that is reflected in the model by assuming a general transition matrix \mathbf{T} .

The need for like-versus-like aggression between dominant individuals for dominance hierarchy reaching ESS lends support to the ‘social control hypothesis’ [38,39], which states that social aggression can maintain the evolutionary stability of status signalling systems. In [38] and [39] it is suggested that a subordinate would encounter relatively more aggression from true dominants as a cheat than as a honest signaller, simply by the fact that dominants are normally fighting each other. As the intrinsic fighting abilities of subordinates on average are lower than those of true dominants, the heightened aggression cheaters would receive would be a cost that would outweigh any benefits arising from increased dominance status. According to this hypothesis, and in order to be evolutionarily stable, the heightened aggression should not result from the ‘persecution’ of cheat by true dominants in the population, but should be the result of dominant individuals interacting more with other dominant birds than with subordinate ones (i.e.: like-versus-like aggression between dominant individuals) [9,39,40]. The social control hypothesis, albeit controversial [9], has been tested in several species and at least for some of them it has been shown to work [8,9,11,38–42]. This view of the social control hypothesis and the presence of like-versus-like aggression suggests signals of status as a form of handicap (see [43]), where only the individuals having a better quality can afford costly badges to demonstrate their high status; the main difference to traditional handicaps is that the cost of a signal of dominance is not direct but an indirect one, mediated by social interactions: dominant individuals are involved in more fights than cheaters (not true dominant birds) would be able to bear [2].

In [11,12] it is suggested that within the context of the social control hypothesis and like-versus-like aggression, both dominants and subordinates have benefits and costs. Subordinates (i.e., small badge size) have no preferential access to food sources, but can enjoy the advantages of their

subordinate status by not receiving too much aggressions from the dominant class [35,44], and dominants (i.e., large badge size), on the other hand, clearly enjoy a preferential access to food, but are engaged in many aggressive interactions [12,35,44]. According to their verbal model, such dichotomization of roles should give two distinct plumage classes [12]. However, our mathematical model suggests that because of interactions with sexual selection, this does not necessarily need to be the rule.

Assuming equal competition coefficients (γ_i) and like-versus-like aggression between dominant and subdominant individuals, the sum of potential survival and fecundity of dominant individuals ($s_3^0 + f_3^0$) should be higher than that of subdominant birds ($s_2^0 + f_2^0$) in order to have $N_3^* > N_2^*$, a necessary condition for bimodality of the frequency distribution of badges of social status. For instance, in the case of a species with a bimodal badge of status as the Siskin, for which dominant individuals do not enjoy a pairing advantage [2], their potential survival should compensate for that and be high since then $f_1^0 = f_2^0 = f_3^0$. In fact, this is what it seems to happen, with dominant individuals showing higher body mass and lower metabolic rate than birds of lower social status [45]. In Red-billed queleas (*Quelea quelea*), for which plumage coloration has also been found to be bimodally distributed and not to have any role in mate choice [46], we should also predict a higher survival potential for the highly ornamented birds, although we have to point out that for this species no role of plumage coloration in social status signalling has yet been described and our model only applies to species showing this status signalling. With respect to the second condition for frequency distribution of badges to be bimodal, $N_1^* > N_2^*$, the model predicts that it will be fulfilled for most of positive equilibria when subordinates are not engaged in many intra-class aggressions ($w_1 \ll 1$). In any case (i.e., for $0 < w_1 \leq 1$), there is no need for subordinates to have a value of the sum of potential survival and fecundity ($s_1^0 + f_1^0$) higher than that of dominants ($s_3^0 + f_3^0$) in order to have a bimodal equilibrium.

Bimodality can also appear in the case of species in which badges of social status additionally have a prominent function as sexual ornaments (i.e., ambivalent characters, [6]), raising in this way the potential reproductive success of dominant individuals ($f_3^0 > f_2^0 > f_1^0$). In this case potential survival of dominant individuals is of minor importance. However, when potential survival for those dominant ornamented individuals is low, frequency distribution of the ornament may shift to a normal shape. This is in fact what seems to happen to most ornamented species, for which the ornament may act as a handicap reducing potential survival [47,48] and consequently shaping their frequency distribution to be normal (Fig. 1). Similarly, when fecundity is independent of the size of the badge of dominance, a high predation (i.e., low survival) for individuals displaying these badges of status (e.g. [9,37,42,49,50]) could also select for normal distributions.

Nevertheless, it is important to distinguish between potential (or inherent) fecundities and survival rates, which are values in a virgin environment without competition among members of the population (i.e., f_i^0 and s_i^0 , respectively), and the values that these rates reach at equilibrium, when competition effects among members of the dominance classes are present (i.e., f_i^* and s_i^* , respectively). For instance, our model predicts that, at the equilibrium determined by the evolutionarily stable strategy, whenever the dominance classes have the same fecundities ($f_1 = f_2 = f_3 = f$), as it is the case of the Siskin [2], the survival rates at the equilibrium for the three classes have also to be equal ($s_1^* = s_2^* = s_3^* = 1 - f$), and this is in fact what it seems to happen (JCS, personal observation). A possible reason for the larger decrease of the survival probability of the dominant individuals at equilibrium with respect to that of the subdominant individuals ($s_3^0 > s_2^0$

while $s_3^* = s_2^*$) is the higher number of aggressive interactions among members of the dominant class. This similar survival for the dominant and subordinate classes would support the view of Maynard Smith of status signalling as a mixed ESS [19], which could additionally explain why cheaters pretending a higher dominance status of the one they have, do not invade the population [2].

Summarizing, we have that the frequency distribution of badges of status may be predicted by the inter-relationship between survival, reproductive and aggression rates of the different dominance classes. This has been nicely exemplified with the Siskin, our model species, for which the bimodality of bib size distribution may be explained by the fact that Siskin females do not choose mates based on this character, but dominant individuals potentially enjoy a survival advantage. Hence our model may allow to understand interspecific variation in frequency distribution of badges of status, and more importantly, helps to understand the roles that shape the evolutionary stability of the system.

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