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Spatial Mendelian games

J. Radcliffe *, L. Rass

School of Mathematical Sciences, Queen Mary and Westfield College, University of London, Mile End Road, London E1 4NS, UK

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Abstract

This paper considers complex models arising in sociobiology. These combine genetic and strategic aspects to model the effect of gene-linked strategies on the ability of individuals to survive to maturity, mate and produce offspring. Several important models considered in the literature are generalised and extended to incorporate a spatial aspect. Individuals are allowed to migrate. Contests, e.g. for food or amongst males for females, take place locally. The choice of the point at which the population structure is measured affects the complexity of the equations describing the system, although it is possible to utilise any point in the life cycle. For our spatial models the simplest approach is to measure the population structure immediately after migration. A saddle point method, developed by the authors, has previously been used to obtain results for simple discrete time spatial models. It is utilised here to obtain the speed of first spread of a new gene-linked strategy for the much more complex sociobiological models included in this paper. This demonstrates the wide-ranging applicability and power of the method. © 1998 Elsevier Science Inc. All rights reserved.

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1. Introduction

Genetic models and game theoretic models have been used to describe evolutionary processes. However until recently models included only one of these

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* Corresponding author. Tel.: +44-171 975 5513/5219; fax: +44-181 981 9587; e-mail: j.radcliffe@qmw.ac.uk.

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aspects, although clearly a model incorporating both games and genetics would be more realistic (see Refs. [1,2] for a critique). Non-spatial models for genetics are described in Ref. [3]; those for evolutionary games being given in Refs. [4,5].

Recently more complex sociobiological models have been formulated in which the genetic and strategic aspects are combined (see Refs. [5–11]). The games can describe symmetric or asymmetric contests. The following two situations are examples of symmetric contests in sociobiology: (i) a single population in which the behaviour of individuals, i.e. the strategies played, depend on the genotypes at a single autosomal locus and (ii) a single population in which only the males play different strategies depending on their genotype. There are many examples of populations in which the males play different strategies in the competition for females. Many species have been observed to exhibit polymorphism which is associated with the playing of different strategies. A three strategy example occurs in side-blotched lizards which have throat-colour polymorphism. Here the strategy adopted by very aggressive males is to defend large territories, other males adopt the strategy of sneaking, whilst the intermediate strategy is to defend smaller territories. This is discussed in detail in Refs. [12,13]. Polymorphism associated with two strategies occurs in bluegill sunfish [14]. Further examples include stoats [15], deer [16], salmon [17–20], ruff [21,22], marine isopods [23] and wrasse [24].

Models can also be set up involving asymmetric contests. These include bimatrix games with two populations which are in competition. In most species of birds and many mammals and fish both parents can spend an appreciable amount of effort in bringing up their offspring. Trivers introduced the concept of parental investment [25], and reviewed situations where this occurs [26]. Parental care, and models to describe it, are discussed in Ref. [4]. An asymmetric game which describes this situation and has received much attention is the battle of the sexes (see Refs. [27–33]). In this model the female strategies, fast and coy, are based on the length of courtship and duration of partnerships formed; the fast female tending to have shorter courtships and less enduring relationships than a coy female. All females are assumed to care for their offspring. The male strategies are based on whether a male is prepared to engage in a long courtship, be faithful and care for its offspring or to be a philanderer, who has many short term relationships with no part in the ensuing care and nurture of offspring produced. A version of this game which incorporates Mendelian genetics has been considered in Refs. [5,6,11]. The analysis of these sociobiological models has at present been confined to the non-spatial case.

In many cases realistic models will need to include a spatial aspect. It has been pointed out by Godfray and Hassell [34] (see also Ref. [35]), that in recent years there has been an increasing realization of the importance of spatial processes in all branches of population dynamics. The importance of the spatial aspect has also been emphasised by Durrett and Levin [36] and Boerlijst and

Hogeweg [37]. Spatial models have been used for some time in genetics. The spatial spread of a new gene has been investigated by means of diffusion models (see Refs. [38–40]) and by the use of migration distributions (see Refs. [41–44]). Spatial models are also increasingly being used in evolutionary game theory (see Refs. [45–55]).

In this paper we set up spatial forms of some of the models described in paragraphs 2 and 3. The models are in discrete time and a migration distribution is used to incorporate the spatial aspect. The spatial dynamics are analagous to those used for purely genetic models by Wienberger [41,42] and Lui [43,44]. Individuals play strategies locally which are governed by their genetic makeup. Survival and success in reproduction are dependent on the strategy played. A migration term is also included in the model. After reproduction, reaping occurs to maintain the constant carrying capacity of the habitat. Initially only one gene is present in each population. A new gene can arise by mutation, or may be introduced from outside. We consider the speed with which such a new gene will spread and modify the pattern of behaviour of the population(s).

The speed of spatial spread has previously been examined in various areas of mathematical biology, including simple genetics and games. There is an exact approach which may be used in simpler contexts to find the asymptotic speed of propagation of a gene/strategy. Results for the spread of a single gene in a discrete time model were obtained by Weinberger [41,42] and Lui [43,44]; whilst corresponding exact results for simple models in evolutionary games were given by Radcliffe and Rass [56].

There is also another approach, which we call the saddle point method. This can be used to obtain the speed of first spread in biological models. It is a very powerful method which enables results to be obtained for much more complex situations, less tractable to exact analysis. The technique was originally applied to a simple continuous time model of a one-type epidemic by Daniels [57]; a rigorised approach suitable for n-type models being given by Radcliffe and Rass [58]. A theoretical treatment of the saddle point method for models of discrete time multi-type processes is given in Ref. [59]. In all situations where an exact result has been proved, the result obtained by the saddle point method agrees with it.

The saddle point method is particularly suitable for the analysis of the complex sociobiological models contained in this present paper. It enables us to obtain an expression for the speed of first spread of a new gene (genotype) and its associated strategy.

2. The saddle point result

The saddle point result for discrete time models was proved by Radcliffe and Rass [59]. In this section we state the saddle point result in a general setting, so that it can be applied in Sections 3–6 to certain spatial models in sociobiology which combine the ideas from genetics and games. The models considered in this paper involve certain types, and $x_i^{(m)}(\mathbf{s})$ denotes the proportion of type i in the mth generation at position $\mathbf{s} \in \mathbb{R}^N$. The type represents a particular allele or genotype. Which of these is used is dependent upon the point in the genetic cycle at which the process is measured. We suppose that initially the population consists of certain types. Other types $n_1 + 1, \dots, n$ are introduced into a bounded region B and the speed of first spread for these types is considered. Far from the region B, the linearised equations in the models considered in this paper are of the form

$$x_i^{(m+1)}(\mathbf{s}) = \sum_{j=n_1+1}^{n} \gamma_{ij} \int_{\mathbb{R}^N} p_{ij}(\mathbf{r}) x_j^{(m)}(\mathbf{s}-\mathbf{r})\, \mathrm{d}r \tag{1}$$

for $i = n_1 + 1, \dots, n$, where the γ_{ij} are non-negative and will depend upon the particular application. It is assumed that the matrix (γ_{ij}) is non-reducible. Individuals are allowed to move, and $p_{ij}(\mathbf{r})$ denotes a migration density representing the vector distance $\mathbf{r}$ moved.

Consider the speed of spread of the forward front in a direction with direction cosines ζ for type $(n_1 + i)$. Take a fixed η, which is small and positive. Then define $s(m)$ so that

$$\int_{\mathbf{u}\,:\,\zeta'\mathbf{u} \geqslant s(m)} x_{n_1+i}^{(m)}(\mathbf{u})\, \mathrm{d}\mathbf{u} = \eta.$$

The speed of first spread of a type $(n_1 + i)$ individual is defined as

$$c = \lim_{m\to\infty} \frac{s(m)}{m}.$$

Let $P_{ij}(\lambda) = \int_{\mathbb{R}^N} \mathrm{e}^{\lambda\zeta'\mathbf{s}} p_{ij}(\mathbf{s})\, \mathrm{d}\mathbf{s}$ and $\{\mathbf{A}(\lambda)\}_{ij} = \gamma_{n_1+i,n_1+j} P_{n_1+i,n_1+j}(\lambda)$. Define $\rho(\mathbf{A}(\lambda))$ to be the Perron–Frobenius root of $\mathbf{A}(\lambda)$.

It is shown in Ref. [59] that the speed c of first spread is given by

$$c = \max\left(0, \inf_{\lambda>0} \frac{\log(\rho(\mathbf{A}(\lambda)))}{\lambda}\right). \tag{2}$$

3. A Mendelian game with two alleles

We first describe the non-spatial model. The behaviour of an individual is determined by two genes A_1 and A_2. The genotypes A_1A_1, A_2A_2 and A_1A_2 play strategies S_1, S_2 and S_3 respectively. The strategy S_3 is likely to be either an intermediate strategy between S_1 and S_2, or to model the situation when the heterozygote plays strategy S_1 with probability p and S_2 with probability $(1 - p)$. The 3 × 3 payoff matrix for the game with strategies S_1, S_2 and S_3 is denoted by $\mathbf{A} = (a_{ij})$. The playing of the strategies result in contests which are not sex specific. This is used to describe a situation in which individuals compete for food [60]. An example of this is the genetic model of the Hawk–Dove game in Ref. [4].

Suppose the proportions of the alleles A_1 and A_2 just prior to the birth of the next generation are x_1 and x_2, with $x_1 + x_2 = 1$. In the next generation the proportions of the genotypes A_1A_1, A_2A_2 and A_1A_2 are $x_1^2,\ x_2^2$ and $2x_1x_2$, respectively. The average payoff to an A_1A_1 genotype is $a_{11}x_1^2 + 2a_{13}x_1x_2 + a_{12}x_2^2$, with similar results for the genotypes A_1A_2 and A_2A_2. For each genotype, we identify the average payoff with its fitness to survive and reproduce.

The model may then be regarded as a genetics model with the frequency dependent fitness matrix

$$\begin{aligned}\mathbf{W}(x_2) &= \begin{pmatrix} a(x_2) & b(x_2) \\ b(x_2) & c(x_2) \end{pmatrix} \\ &= \begin{pmatrix} a_{11}x_1^2 + 2a_{13}x_1x_2 + a_{12}x_2^2 & a_{31}x_1^2 + 2a_{33}x_1x_2 + a_{32}x_2^2 \\ a_{31}x_1^2 + 2a_{33}x_1x_2 + a_{32}x_2^2 & a_{21}x_1^2 + 2a_{23}x_1x_2 + a_{22}x_2^2 \end{pmatrix}, \end{aligned} \tag{3}$$

where $x_1 = 1 - x_2$.

Let $\{\mathbf{x}^{(m)}\}_i = x_i^{(m)}$, where $x_i^{(m)}$ is the proportion of allele A_i in the mth generation. The model is described by the equations

$$x_i^{(m+1)} = \frac{x_i^{(m)}\left\{\mathbf{W}(x_2^{(m)})\mathbf{x}^{(m)}\right\}_i}{\mathbf{x}^{(m)\prime}\mathbf{W}(x_2^{(m)})\mathbf{x}^{(m)}}, \quad i = 1,2.$$

Since $x_1^{(m)} + x_2^{(m)} = 1$ we need only consider the second equation, which may be written in the form

$$x_2^{(m+1)} = g\left(x_2^{(m)}\right), \tag{4}$$

where

$$g(\theta) = \frac{c(\theta)\theta^2 + b(\theta)\theta(1-\theta)}{c(\theta)\theta^2 + 2b(\theta)\theta(1-\theta) + a(\theta)(1-\theta)^2} \tag{5}$$

with $a(\theta),\ b(\theta)$ and $c(\theta)$ given by Eq. (3).

Consider the local stability of $(x_1, x_2) = (1,0)$, when it is initially disturbed by a small amount. Using the usual techniques, it can be shown that the point is locally stable if $g'(0) < 1$, i.e. $a_{31}/a_{11} < 1$. In this case, when a small proportion of gene A_2 is introduced into a population where only gene A_1 was originally present, the gene A_2 and the associated strategies S_2 and S_3 will not become established and will die out.

We now describe the spatial model. Consider the speed of spread of gene A_2, which is introduced into a bounded region B of $\mathbb{R}^N$, through a population in which initially only the gene A_1 is present. A habitat is considered which has constant carrying capacity at all points of $\mathbb{R}^N$. Consider the composition of the alleles for generation m at position $\mathbf{s}$ prior to mating. Let $x_i^{(m)}(\mathbf{s})$ denote the proportion of the gene A_i at position $\mathbf{s}$ in the mth generation. Random mating occurs at each position $\mathbf{s}$, the number of offspring being unaffected by the genotype. An individual at position $\mathbf{r}$ plays against the individuals in its vicinity. If it is assumed that an individual at position $\mathbf{r}$ plays only against individuals at position $\mathbf{r}$, the survival to maturity of the genotypes at position $\mathbf{r}$ is governed by a fitness matrix $\mathbf{W}(x_2^{(m)}(\mathbf{r}))$.

Reaping occurs to reduce the population to the carrying capacity of the habitat. Migration then takes place with $p(\mathbf{r})$ being the probability density function corresponding to migration by a vector distance $\mathbf{r}$. A new generation is produced and the previous generation dies.

The model is described by the equation

$$x_2^{(m+1)}(\mathbf{s}) = \int\limits_{\mathbb{R}^N} p(\mathbf{s}-\mathbf{r})g\left(x_2^{(m)}(\mathbf{r})\right)\,\mathrm{d}\mathbf{r}, \tag{6}$$

where $g(\theta)$ is given by Eq. (5).

The linearisation of $g(\theta)$ is ((constant term in b$(\theta))\theta)/($constant term in a$(\theta))$, where $a(\theta) = a_{11}(1-\theta)^2 + 2a_{13}(1-\theta)\theta + a_{12}\theta^2$ and $b(\theta) = a_{31}(1-\theta)^2 + 2a_{33}(1-\theta)\theta + a_{32}\theta^2$. Thus, for small θ, $g(\theta)$ is approximately $(a_{31}/a_{11})\theta$. In the forward front, where $x_2^{(m)}(\mathbf{r})$ is small, the approximate equation is given by

$$x_2^{(m+1)}(\mathbf{s}) = \gamma\int\limits_{\mathbb{R}^N} p(\mathbf{s}-\mathbf{r})x_2^{(m)}(\mathbf{r})\,\mathrm{d}\mathbf{r}, \tag{7}$$

where $\gamma = (a_{31}/a_{11})$.

Rather than assume that an individual at position $\mathbf{r}$ plays only against individuals at position $\mathbf{r}$, it would be more realistic to allow the individual to play against individuals at various positions in its vicinity. In this setup we could assume that the payoff to an A_1A_1 genotype can be expressed as $\int(a_{11}x_1^2(\mathbf{u}) + 2a_{13}x_1(\mathbf{u})x_2(\mathbf{u}) + a_{12}x_2^2(\mathbf{u}))q(\mathbf{r}-\mathbf{u})\,\mathrm{d}\mathbf{u}$, where $q(\mathbf{u})$ represents the probability density function of a contact vector random variable C. The payoffs to A_2A_2 and A_1A_2 genotypes are $\int(a_{21}x_1^2(\mathbf{u}) + 2a_{23}x_1(\mathbf{u})x_2(\mathbf{u}) + a_{22}x_2^2(\mathbf{u}))q(\mathbf{r}-\mathbf{u})\,\mathrm{d}\mathbf{u}$ and $\int(a_{31}x_1^2(\mathbf{u}) + 2a_{33}x_1(\mathbf{u})x_2(\mathbf{u}) + a_{32}x_2^2(\mathbf{u}))q(\mathbf{r}-\mathbf{u})\,\mathrm{d}\mathbf{u}$, respectively. However, if an individual plays against other individuals which are nearby, it can be assumed that the variance-covariance matrix of the contact vector random variable C has reasonably small entries. Then in the forward front, the approximate equation is still given by Eq. (7).

It follows from the general result of Section 2 that the speed c of first spread of gene A_2 is given by

$$c = \max\left(0, \inf_{\lambda>0}\left(\frac{\log(P(\lambda)) + \log(a_{31}/a_{11})}{\lambda}\right)\right), \tag{8}$$

where $P(\lambda)$ is the Laplace transform of the projected migration distribution. Note that when a small amount of gene A_2 is present, it occurs predominantly in the heterozygote A_1A_2. If equations for the genotypes are considered, as in Sections 5 and 6, then the approximation in the forward front is valid only for the heterozygote A_1A_2 and not for the homozygote A_2A_2. The speed of first spread of gene A_2 is therefore that of the heterozygote and hence of strategy S_3. When $a_{31}/a_{11} < 1$, then for any contact distribution

$$\lim_{\lambda\downarrow 0}\left(\frac{\log(P(\lambda)) + \log(a_{31}/a_{11})}{\lambda}\right) = -\infty.$$

Thus the speed of first spread of the forward front is zero. The condition $a_{31}/a_{11} < 1$ corresponds in the non-spatial case to $(x_1, x_2) = (1,0)$ being locally stable.

When $a_{31}/a_{11} > 1$, in the non-spatial case $(x_1, x_2) = (1,0)$ is unstable and the gene A_2 when introduced into the population can never die out. In the spatial model the speed of first spread will be positive for all directions provided the contact distribution is radially symmetric.

The remaining case has $a_{31}/a_{11} = 1$. Note that, as $\lambda \downarrow 0$, $g(\lambda) = \log(P(\lambda))/\lambda$ tends to $\mu = P'(0)$ and $g'(\lambda)$ tends to $\sigma^2/2$, where μ and σ^2 are the mean and variance of the projection of the migration distribution in direction ζ. Also $g(\lambda)$ has no maximum for $\lambda > 0$ so that $\inf_{\lambda>0} g(\lambda) = \lim_{\lambda\downarrow 0} g(\lambda)$. Thus when the mean μ is positive, it gives the speed of first spread. Otherwise the speed is zero; this latter case in particular occurs when the contact distribution is radially symmetric.

The following variation of this setup can be analysed in a similar manner. We first describe the non-spatial model. The behaviour of an individual is determined by two genes A_1 and A_2, where the gene A_1 predisposes an individual to play strategy S_1 and A_2 to play S_2. It is assumed that the homozygotes A_1A_1 and A_2A_2 play strategies S_1 and S_2 respectively, while the hetrozygote A_1A_2 plays the random strategy which consists of playing S_1 with probability p and playing S_2 with probability $(1 - p)$. The 2×2 payoff matrix is denoted by $\mathbf{A} = (a_{ij})$. The fitness matrix is given by

$$\mathbf{W} = \begin{pmatrix} a_{11}x_1 + a_{12}x_2 & (pa_{11} + (1-p)a_{21})x_1 + (pa_{12} + (1-p)a_{22})x_2 \\ (pa_{11} + (1-p)a_{21})x_1 + (pa_{12} + (1-p)a_{22})x_2 & a_{21}x_1 + a_{22}x_2 \end{pmatrix}. \tag{9}$$

The corresponding spatial model leads to Eq. (7) with γ now given by $\gamma = ((pa_{11} + (1-p)a_{21})/a_{11})$ and the speed c of first spread of gene A_2 is given by

$$c = \max\left(0, \inf_{\lambda>0}\left(\frac{\log P(\lambda) + \log((pa_{11} + (1-p)a_{21})/a_{11})}{\lambda}\right)\right). \tag{10}$$

The expression for c given by Eq. (10) can be obtained from Eq. (8) by replacing a_{31} by $p(a_{11} + (1-p)a_{21})$. This is the average payoff corresponding to replacing the strategy S_3, played by the hetrozygote A_1A_2, by the mixed strategy where S_1 and S_2 are played with probabilities p and $(1-p)$, respectively.

Note that in the forward front most individuals play S_1. So that in the forward front the system is behaving like a genetics model with fitness matrix

$$\mathbf{V} = \begin{pmatrix} v_{11} & v_{12} \\ v_{12} & v_{22} \end{pmatrix} = \begin{pmatrix} a_{11} & pa_{11} + (1-p)a_{21} \\ pa_{11} + (1-p)a_{21} & a_{21} \end{pmatrix}.$$

A simple expression for the speed, c, of first spread can be obtained in the particular case where the projection of the contact distribution in direction ζ is normally distributed with mean μ and variance σ^2. The speed is given by $c = \max\left(0, \mu + \sigma\sqrt{2\log(\gamma)}\right)$, where $\gamma = a_{31}/a_{11}$ for the first model and $\gamma = (pa_{11} + (1-p)a_{21})/a_{11}$ for the second model.

4. Competition between two populations

Consider two populations P_1 and P_2 which are in competition. There are various situations that can be modelled describing competition between two populations, (see Ref. [6]). We consider the setup where all individuals in population P_1 play against all individuals in population P_2. In population P_1 the genotypes A_1A_1, A_2A_2 and A_1A_2 play strategies S_1, S_2 and S_3 respectively. In population P_2 the genotypes B_1B_1, B_2B_2 and B_1B_2 play strategies T_1, T_2 and T_3 respectively. If an individual in P_1 plays S_i against an individual in P_2 playing T_j, the individual in P_1 has payoff a_{ij} and the individual in P_2 has payoff b_{ji}. Here S_3 and T_3 are likely either to be intermediate strategies between those of the homozygotes, or to be combined strategies. The heterozygote would the play strategy S_1 (or T_1), with probability p (or q) and otherwise would play the strategy S_2 (or T_2).

Suppose the proportions of the alleles A_1 and A_2 in population P_1 just prior to the birth of the next generation are x_1 and x_2; and the corresponding proportions of the alleles B_1 and B_2 in population P_2 are y_1 and y_2.

The fitness matrix $\mathbf{V}(y_2)$ for the genotypes A_1A_1, A_1A_2 and A_2A_2 of population P_1 is given by

$$\begin{aligned} \mathbf{V}(y_2) &= \begin{pmatrix} a(y_2) & b(y_2) \\ b(y_2) & c(y_2) \end{pmatrix} \\ &= \begin{pmatrix} a_{11}y_1^2 + 2a_{13}y_1y_2 + a_{12}y_2^2 & a_{31}y_1^2 + 2a_{33}y_1y_2 + a_{32}y_2^2 \\ a_{31}y_1^2 + 2a_{33}y_1y_2 + a_{32}y_2^2 & a_{21}y_1^2 + 2a_{23}y_1y_2 + a_{22}y_2^2 \end{pmatrix}, \end{aligned} \tag{11}$$

where $y_1 = 1 - y_2$.

Let the fitness matrix $\mathbf{W}(x_2)$ for the genotypes B_1B_1, B_1B_2 and B_2B_2 of population P_2 be given by

$$\begin{aligned}\mathbf{W}(x_2) &= \begin{pmatrix} d(x_2) & e(x_2) \\ e(x_2) & f(x_2) \end{pmatrix} \\ &= \begin{pmatrix} b_{11}x_1^2 + 2b_{13}x_1x_2 + b_{12}x_2^2 & b_{31}x_1^2 + 2b_{33}x_1x_2 + b_{32}x_2^2 \\ b_{31}x_1^2 + 2b_{33}x_1x_2 + b_{32}x_2^2 & b_{21}x_1^2 + 2b_{23}x_1x_2 + b_{22}x_2^2 \end{pmatrix},\end{aligned} \tag{12}$$

where $x_1 = 1 - x_2$.

Let $x_2^{(m)}$ and $y_2^{(m)}$ be the proportions of allele A_2 in population P_1 and allele B_2 in population P_2 respectively in the mth generation. The model is described by the equations

$$\begin{aligned} x_2^{(m+1)} &= g\left(x_2^{(m)}, y_2^{(m)}\right), \\ y_2^{(m+1)} &= h\left(x_2^{(m)}, y_2^{(m)}\right), \end{aligned} \tag{13}$$

where

$$\begin{aligned} g(\theta, \phi) &= \frac{c(\phi)\theta^2 + b(\phi)\theta(1-\theta)}{c(\phi)\theta^2 + 2b(\phi)\theta(1-\theta) + a(\phi)(1-\theta)^2}, \\ h(\theta, \phi) &= \frac{f(\theta)\phi^2 + e(\theta)\phi(1-\phi)}{f(\theta)\phi^2 + 2e(\theta)\phi(1-\phi) + d(\theta)(1-\phi)^2}. \end{aligned}$$

Consider the local stability of $(x_1, x_2) = (1, 0)$ if gene A_2 is introduced into population P_1 when initially only A_1 and B_1 are present in populations P_1 and P_2. The point is locally stable if $a_{31} < a_{11}$. Similarly if gene B_2 is introduced instead of gene A_2, the point $(y_1, y_2) = (1, 0)$ is locally stable if $b_{31} < b_{11}$. When both genes A_2 and B_2 are introduced, the point $(x_1, x_2, y_1, y_2) = (1, 0, 1, 0)$ is locally stable provided both $a_{31} < a_{11}$ and $b_{31} < b_{11}$.

Now consider the spatial model. Let $x_i^{(m)}(\mathbf{s})$ and $y_i^{(m)}(\mathbf{s})$ measure the proportion in generation m at position $\mathbf{s}$ respectively of the allelle A_i in population P_1 and the allelle B_i in population P_2. Random mating then occurs within each population. Individuals grow up and compete, their survival to maturity and ability to reproduce being governed by the fitness matrix $\mathbf{V}(\mathbf{y}_2^{(m)}(\mathbf{r}))$ and $\mathbf{W}(\mathbf{x}_2^{(m)}(\mathbf{r}))$. Migration then occurs, the density for migration by a distance $\mathbf{r}$ being $p(\mathbf{r})$ and $q(\mathbf{r})$ for populations P_1 and P_2 respectively. The spatial model is described by the equations

$$\begin{aligned} x_2^{(m+1)}(\mathbf{s}) &= \int_{\mathbb{R}^N} p(\mathbf{s} - \mathbf{r}) g\left(x_2^{(m)}(\mathbf{r}), y_2^{(m)}(\mathbf{r})\right) \, \mathrm{d}\mathbf{r}, \\ y_2^{(m+1)}(\mathbf{s}) &= \int_{\mathbb{R}^N} q\Big(\mathbf{s} - \mathbf{r}) h(x_2^{(m)}(\mathbf{r}), y_2^{(m)}(\mathbf{r})\Big) \, \mathrm{d}\mathbf{r}, \end{aligned} \tag{14}$$

where $p(\mathbf{r})$ and $q(\mathbf{r})$ are the migration distributions for individuals in the populations P_1 and P_2 respectively.

We first consider the spread of allele A_2 when it is introduced into a bounded region of $\mathbf{R}^N$, where only A_1 and B_1 are present initially. Then outside this bounded region, $y_2^{(m+1)}(\mathbf{s}) \equiv 0$. Hence in the forward front the approximate equation is

$$x_2^{(m+1)}(\mathbf{s}) = \frac{a_{31}}{a_{11}} \int\limits_{\mathbb{R}^N} p(\mathbf{s}-\mathbf{r}) x_2^{(m)}(\mathbf{r})\, \mathrm{d}\mathbf{r}. \tag{15}$$

It follows that the speed of first spread of gene A_2, and hence of genotype A_1A_2 and strategy S_3, is given by

$$c_1 = \max\left(0, \inf_{\lambda>0}\left(\frac{\log(P(\lambda)) + \log(a_{31}/a_{11})}{\lambda}\right)\right), \tag{16}$$

where $P(\lambda)$ is the Laplace transform of the projected migration distribution for population P_1. This speed is zero if $a_{31} < a_{11}$, the condition for local stability in the non-spatial model. The corresponding result for the speed of first spread of allele B_2, genotype B_1B_2 and strategy T_2 when only A_1 and B_1 were present initially is

$$c_2 = \max\left(0, \inf_{\lambda>0}\left(\frac{\log(Q(\lambda)) + \log(b_{31}/b_{11})}{\lambda}\right)\right). \tag{17}$$

Here $Q(\lambda)$ is the Laplace transform of the projected migration distribution for population P_2.

If both alleles A_2 and B_2 are introduced into a population in which only A_1 and B_1 are present initially, the system cannot be linearised in the forward front for the allele who's natural speed of spread is slower, i.e. it cannot be linearised for allele A_2 when $a_{31}/a_{11} > b_{31}/b_{11}$ and vice versa. The saddle point method gives the speed of first spread of allele A_2 and strategy S_3 as c_1 provided $a_{31}/a_{11} \geqslant b_{31}/b_{11}$. It gives the speed of first spread of allele B_2 and strategy T_3 as c_2 provided $a_{31}/a_{11} \leqslant b_{31}/b_{11}$. When the contact distributions are symmetric at least one new strategy will spread in a specified direction if at least one of the conditions $a_{31} > a_{11}$ and $b_{31} > b_{11}$ holds. This is the condition for local instability of the point (x_1, x_2, y_1, y_2) in the non-spatial case.

As in Section 3, games may be played locally. Also the variation may be considered in which the genotype A_1A_2 plays a random strategy. A further adaptation of this model allows only the males of P_1 to compete with the males of P_2. This can be treated in a similar fashion and the speed of first spread obtained.

5. A model with contests between males

We first describe the non-spatial model. Consider a population consisting of males and females. When the individuals in a generation reach maturity, the males compete with each other for females. We assume that the only selection mechanism that operates occurs at this stage and operates within the male population only. A model of a population in which there are contests between males for females has been considered by Hofbauer et al. [9]. Only the males play different strategies. The male genotypes A_1A_1, A_2A_2 and A_1A_2 play strategies S_1, S_2 and S_3, respectively. The 3×3 payoff matrix is denoted by $\mathbf{A} = (a_{ij})$.

References to a number of species in which contests between males occur are given in paragraph 2 of the introduction. In some cases there are three distinct male strategies, whilst in others there are only two. In the latter case the heterozygote is assumed to play the homozygotic strategies with probabilities p and $(1-p)$. An example of alternative strategies are defending different sized territories and sneaking.

We assume that an offspring is equally likely to be male or female. Denote the genotypes 1, 2 and 3 by A_1A_1, A_2A_2 and A_1A_2, respectively. Let the proportions of the ith genotype in the mth generation for both male and female populations, after birth and before male selection takes place, be $x_i^{(m)}$, $(i = 1, 2, 3)$. During male selection, the average payoff to a male with the ith genotype is $\{\mathbf{Ax}^{(m)}\}_i$, $(i = 1, 2, 3)$. Thus after male selection, the proportion of this male genotype becomes $z_i^{(m)} = (\{\mathbf{Ax}^{(m)}\}_i x_i^{(m)})/(\mathbf{x}^{(m)\prime}\mathbf{Ax}^{(m)})$, $(i = 1, 2, 3)$. Females are unaffected by selection.

The proportions of genotypes in the next generation for both male and female populations, are given by

$$\begin{aligned}
x_1^{(m+1)} &= \left(z_1^{(m)} + \frac{1}{2}z_3^{(m)}\right)\left(x_1^{(m)} + \frac{1}{2}x_3^{(m)}\right),\\
x_2^{(m+1)} &= \left(z_2^{(m)} + \frac{1}{2}z_3^{(m)}\right)\left(x_2^{(m)} + \frac{1}{2}x_3^{(m)}\right),\\
x_3^{(m+1)} &= \left(z_1^{(m)} + \frac{1}{2}z_3^{(m)}\right)\left(x_2^{(m)} + \frac{1}{2}x_3^{(m)}\right) + \left(z_2^{(m)} + \frac{1}{2}z_3^{(m)}\right)\left(x_1^{(m)} + \frac{1}{2}x_3^{(m)}\right).
\end{aligned} \tag{18}$$

Consider the local stability of the point $(x_1, x_2, x_3) = (1, 0, 0)$. When a small amount of gene A_2 is introduced, after one generation it will always occur predominantly in the heterozygote. It is easily shown that the point is locally stable if $a_{31} < a_{11}$. When $a_{31} > a_{11}$, once A_2 is introduced it will persist, so that strategy S_2 will also persist in the population. Provided that in addition $a_{32} > a_{22}$, strategy S_3 also persists, since in this case both genes A_1 and A_2 will not die out.

In the spatial model individuals grow up at the position where they were born. Upon reaching maturity they migrate, the migration density differing for males and females. It is convenient to measure the proportion of the three genotypes at position $\mathbf{s}$ in each of the male and female populations at this point in the cycle, i.e. just after they have migrated. The respective proportions of the

ith genotype in generation m are denoted by $x_i^{(m)}(\mathbf{s})$ and $y_i^{(m)}(\mathbf{s})$. Selection of the males then takes place, followed by mating. A new generation is born and grows to maturity. Migration then occurs. Let $z_i^{(m)}(\mathbf{r}) = (\{\mathbf{A}\mathbf{x}^{(m)}(\mathbf{r})\}_i x_i^{(m)}(\mathbf{r}))/(\mathbf{x}^{(m)\prime}(\mathbf{r})\mathbf{A}\mathbf{x}^{(m)}(\mathbf{r}))$, $(i = 1, 2, 3)$.

The equations giving the proportions of male genotypes in the next generation are

$$\begin{aligned}
x_1^{(m+1)}(\mathbf{s}) &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(z_1^{(m)}(\mathbf{r}) + \frac{1}{2}z_3^{(m)}(\mathbf{r})\right)\left(y_1^{(m)}(\mathbf{r}) + \frac{1}{2}y_3^{(m)}(\mathbf{r})\right)\,\mathrm{d}\mathbf{r},\\
x_2^{(m+1)}(\mathbf{s}) &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(z_2^{(m)}(\mathbf{r}) + \frac{1}{2}z_3^{(m)}(\mathbf{r})\right)\left(y_2^{(m)}(\mathbf{r}) + \frac{1}{2}y_3^{(m)}(\mathbf{r})\right)\,\mathrm{d}\mathbf{r},\\
x_3^{(m+1)}(\mathbf{s}) &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\Bigg(\left(z_1^{(m)}(\mathbf{r}) + \frac{1}{2}z_3^{(m)}(\mathbf{r})\right)\left(y_2^{(m)}(\mathbf{r}) + \frac{1}{2}y_3^{(m)}(\mathbf{r})\right)\\
&\quad + \left(z_2^{(m)}(\mathbf{r}) + \frac{1}{2}z_3^{(m)}(\mathbf{r})\right)\left(y_1^{(m)}(\mathbf{r}) + \frac{1}{2}y_3^{(m)}(\mathbf{r})\right)\Bigg)\,\mathrm{d}\mathbf{r},
\end{aligned} \tag{19}$$

where $p_{\mathrm{M}}(\mathbf{r})$ and $p_{\mathrm{F}}(\mathbf{r})$ are the migration densities of female and male individuals, respectively.

The three equations for the female genotypes $y_i^{(m+1)}(\mathbf{s})$, $(i = 1, 2, 3)$, are obtained from Eq. (19) by replacing the $x_i^{(m+1)}(\mathbf{s})$ on the left hand side by $y_i^{(m+1)}(\mathbf{s})$, and replacing $p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})$ by $p_{\mathrm{F}}(\mathbf{s}-\mathbf{r})$ on the right hand side.

Consider how an allele A_2, which is introduced into a bounded region $B \in \mathbb{R}^N$, propagates through a population in which initially only allele A_1 is present. In the forward front, allele A_2 occurs predominantly in the heterozygote. We therefore consider the approximate equations for genotype 3 in the forward front. These are

$$\begin{aligned}
x_3^{(m+1)}(\mathbf{s}) &= \frac{1}{2}\int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\frac{a_{31}}{a_{11}}x_3^{(m)}(\mathbf{r}) + y_3^{(m)}(\mathbf{r})\right)\,\mathrm{d}\mathbf{r},\\
y_3^{(m+1)}(\mathbf{s}) &= \frac{1}{2}\int\limits_{\mathbb{R}^N} p_{\mathrm{F}}(\mathbf{s}-\mathbf{r})\left(\frac{a_{31}}{a_{11}}x_3^{(m)}(\mathbf{r}) + y_3^{(m)}(\mathbf{r})\right)\,\mathrm{d}\mathbf{r}.
\end{aligned}$$

For this model the matrix $\mathbf{A}(\lambda)$ is given by

$$\mathbf{A}(\lambda) = \frac{1}{2}\begin{pmatrix} (a_{31}/a_{11})P_{\mathrm{M}}(\lambda) & P_{\mathrm{M}}(\lambda) \\ (a_{31}/a_{11})P_{\mathrm{F}}(\lambda) & P_{\mathrm{F}}(\lambda) \end{pmatrix} \tag{20}$$

and hence $\rho(\mathbf{A}(\lambda)) = \frac{1}{2}((a_{31}/a_{11})P_{\mathrm{M}}(\lambda) + P_{\mathrm{F}}(\lambda))$, where $P_{\mathrm{M}}(\lambda)$ and $P_{\mathrm{F}}(\lambda)$ are the Laplace transforms of the projected contact distributions for males and females, respectively. It follows from the general result of Section 2 that the speed of first spread of genotype 3, and hence for allele A_2 and strategy S_3, is given by

$$c = \max\left(0, \inf_{\lambda>0}\left(\frac{\log\left(\frac{a_{31}}{a_{11}}P_{\mathrm{M}}(\lambda) + P_{\mathrm{F}}(\lambda)\right) - \log 2}{\lambda}\right)\right). \tag{21}$$

This speed is zero if $a_{31} < a_{11}$, the condition for local stability in the non-spatial model.

Note that it is possible to consider the model at a different point in the cycle. One can work with alleles only if the point in the cycle chosen is just after selection, before mating. The exact equations are more complex, but the equation in the forward front is reasonably simple and leads to the same speed of first spread. This spread of spread is that of the heterozygote and so will be that of strategy S_3. The method does not yield the speed of spread of strategy S_2 for the homozygote since it is not possible to obtain an approximate linear equation which is valid for genotype 2 in the forward front.

The model of this section can easily be modified to encompass the situation where the male A_1A_2 genotype plays a random strategy consisting of playing the strategies S_1 and S_2 with probabilities p and $(1-p)$, respectively. Strategy S_2 will then spread with speed c given by Eq. (21). In this equation $a_{31} = pa_{11} + (1-p)a_{21}$ where a_{11} and a_{21} are the payoffs to an individual playing strategies S_1 and S_2 respectively against an individual playing strategy S_1.

The present approach could have been used in Sections 3 and 4. However, the approach we chose to use in those sections was simpler since the models could be easily expressed in terms of the alleles, as the new generation is in Hardy–Weinberg equilibrium after mating. This is no longer the case for the present model.

6. A genetic model for the battle of the sexes

Maynard Smith and Hofbauer [11] (see also Refs. [5,6]) proposed a genetic model based on the battle of the sexes game. This game is used as a model for parental investment when bringing up offspring. We first describe a generalisation of the model considered by Maynard Smith and Hofbauer and then add a spatial aspect.

The population consists of males and females. There are two pairs of genes, A_1 and A_2 at locus A, and B_1 and B_2 at locus B. Independence of the loci is assumed (no linkage). Males can play three strategies, which depends only on their genotype at the A locus, not on the B locus. Males with genotypes A_1A_1, A_2A_2 and A_1A_2, respectively, play strategies S_1, S_2 and S_3. In the female population the strategies depend only upon the B locus. Females with genotypes B_1B_1, B_2B_2 and B_1B_2 play strategies T_1, T_2 and T_3, respectively. An example of typical strategies are philanderer/faithful for homozygotic males and fast/coy for homozygotic females. The heterozygotes play the homozygotic strategies with probabilities p and $(1-p)$ for males and q and $(1-q)$ for females.

Let the payoff matrix be $\mathbf{V} = (v_{ij})$ for males playing strategies S_1, S_2 and S_3. The corresponding payoff matrix for females playing strategies T_1, T_2 and T_3 is $\mathbf{W}'$ where $\mathbf{W} = (w_{ij})$. The combined payoffs are then given by

	T_1	T_2	T_3
S_1	(v_{11}, w_{11})	(v_{12}, w_{12})	(v_{13}, w_{13})
S_2	(v_{21}, w_{21})	(v_{22}, w_{22})	(v_{23}, w_{23})
S_2	(v_{31}, w_{31})	(v_{32}, w_{32})	(v_{33}, w_{33})

Suppose the entries of $\mathbf{x}_A^{(m)}$ and $\mathbf{x}_B^{(m)}$ give the proportions of genotypes A_{11}, A_{22} and A_{12}, and B_{11}, B_{22} and B_{12} in the male population just after the birth of the mth generation. The corresponding vectors of proportions in the female population are identical to those in the male population.

After selection the proportions of genotypes A_{11}, A_{22} and A_{12} for males are scaled, respectively, by the three entries of $\mathbf{V}\mathbf{x}_B^{(m)}/\mathbf{x}_A^{(m)'}\mathbf{V}\mathbf{x}_B^{(m)}$. The proportions of genotypes B_{11}, B_{22} and B_{12} for females are scaled, respectively, by the three entries of $\mathbf{W}'\mathbf{x}_A^{(m)}/\mathbf{x}_B^{(m)'}\mathbf{W}'\mathbf{x}_A^{(m)}$. The proportions for genotypes B_{11}, B_{22} and B_{12} in the male population and A_{11}, A_{22} and A_{12} in the female population remain unaltered.

Random mating now takes place. For the next generation the genetic structure is identical for males and females. Using independence of the loci (no linkage) an expression for the proportions of genotypes A_{11}, A_{22} and A_{12} and B_{11}, B_{22} and B_{12} is easily obtained. This leads to the following equations for the proportions of the A genotypes in generation $m+1$:

$$\begin{aligned}
\left\{x_A^{(m+1)}\right\}_1 &= \left(\left\{\mathbf{z}_A^{(m)}\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}\right\}_3\right)\left(\left\{\mathbf{x}_A^{(m)}\right\}_1 + \frac{1}{2}\left\{\mathbf{x}_A^{(m)}\right\}_3\right), \\
\left\{x_A^{(m+1)}\right\}_2 &= \left(\left\{\mathbf{z}_A^{(m)}\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}\right\}_3\right)\left(\left\{\mathbf{x}_A^{(m)}\right\}_2 + \frac{1}{2}\left\{\mathbf{x}_A^{(m)}\right\}_3\right), \\
\left\{x_A^{(m+1)}\right\}_3 &= \left(\left(\left\{\mathbf{z}_A^{(m)}\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}\right\}_3\right)\left(\left\{\mathbf{x}_A^{(m)}\right\}_2 + \frac{1}{2}\left\{\mathbf{x}_A^{(m)}\right\}_3\right)\right. \\
&\qquad \left. + \left(\left\{\mathbf{z}_A^{(m)}\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}\right\}_3\right)\left(\left\{\mathbf{x}_A^{(m)}\right\}_1 + \frac{1}{2}\left\{\mathbf{x}_A^{(m)}\right\}_3\right)\right),
\end{aligned} \tag{22}$$

where $\{\mathbf{z}_A^{(m)}\}_i = \{\mathbf{x}_A^{(m)}\}_i\{\mathbf{V}\mathbf{x}_B^{(m)}\}_i/\mathbf{x}_A^{(m)'}\mathbf{V}\mathbf{x}_B^{(m)}$. There are equivalent equations for the B genotypes which are obtained by replacing $\mathbf{x}_A^{(j)}$ by $\mathbf{x}_B^{(j)}$ for $j = m, m+1$ and by replacing $\mathbf{z}_A^{(m)}$ by $\mathbf{z}_B^{(m)}$, where $\{\mathbf{z}_B^{(m)}\}_i = \{\mathbf{x}_B^{(m)}\}_i\{\mathbf{W}'\mathbf{x}_A^{(m)}\}_i/\mathbf{x}_B^{(m)'}\mathbf{W}'\mathbf{x}_A^{(m)}$.

Consider stability when initially only A_1 and B_1 are present. This point is locally stable when gene A_2 is introduced if $v_{31} < v_{11}$. It is locally stable when B_2 is introduced provided $w_{13} < w_{11}$. When both A_2 and B_2 are introduced, local stability occurs if both $v_{31} < v_{11}$ and $w_{13} < w_{11}$.

A spatial version of this model can be written down in a similar manner to the models considered in Section 5. Individuals grow up at the position where they were born. Upon reaching maturity they migrate, the migration density differing for males and females. Let $p_{\mathrm{M}}(\mathbf{r})$ and $p_{\mathrm{F}}(\mathbf{r})$ represent the densities of migration by a vector distance $\mathbf{r}$ for males and females. We measure the proportion of the three genotypes for A and B at position $\mathbf{s}$ in each of the male and female populations just after they have migrated.

Let the entries of $\mathbf{x}_A^{(m)}(\mathbf{s})$ and $\mathbf{x}_B^{(m)}(\mathbf{s})$ give the proportions in generation m at position $\mathbf{s}$ for genotypes $A_{11},\ A_{22}$ and A_{12}, and $B_{11},\ B_{22}$ and B_{12}, respectively, in the male population after a new generation has grown to maturity and migrated but selection is yet to take place. The corresponding vectors of proportions in the female population are denoted by $\mathbf{y}_A^{(m)}(\mathbf{s})$ and $\mathbf{y}_B^{(m)}(\mathbf{s})$.

Selection of the males and females then takes place, followed by mating. A new generation is born and grows to maturity. Migration then occurs.

After selection the proportions of genotypes $A_{11},\ A_{22}$ and A_{12} at position $\mathbf{s}$ for males are scaled respectively by the three entries of $\mathbf{V}\mathbf{y}_B^{(m)}(\mathbf{s})/((\mathbf{x}_A^{(m)}(\mathbf{s}))'\mathbf{V}\mathbf{y}_B^{(m)}(\mathbf{s}))$. The proportions of genotypes $B_{11},\ B_{22}$ and B_{12} at position $\mathbf{s}$ for females are scaled respectively by the three entries of $\mathbf{W}'\mathbf{x}_A^{(m)}(\mathbf{s})/((\mathbf{y}_B^{(m)}(\mathbf{s}))'\mathbf{W}'\mathbf{x}_A^{(m)}(\mathbf{s}))$. The proportions at position $\mathbf{s}$ for genotypes $B_{11},\ B_{22}$ and B_{12} in the male population and $A_{11},\ A_{22}$ and A_{12} in the female population remain unaltered.

Random mating now takes place. For the next generation the genetic structure is identical for males and females just after birth. The individuals then grow to maturity and migrate. The equations giving the proportions at position $\mathbf{s}$ in generation $m+1$ for genotypes $A_{11},\ A_{22}$ and A_{12} and $B_{11},\ B_{22}$ and B_{12} for males is then

$$\begin{aligned}
\left\{x_A^{(m+1)}(\mathbf{s})\right\}_1 &= \int_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_3\right) \\
&\quad \times \left(\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{r}, \\
\left\{x_A^{(m+1)}(\mathbf{s})\right\}_2 &= \int_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_3\right) \\
&\quad \times \left(\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{r}, \\
\left\{x_A^{(m+1)}(\mathbf{s})\right\}_3 &= \int_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left(\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_3\right)\right. \\
&\quad \times \left(\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right) + \left(\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_3\right) \\
&\quad \left.\times \left(\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right)\right) \mathrm{d}\mathbf{r},
\end{aligned}$$

$$\begin{aligned}
\left\{x_B^{(m+1)}(\mathbf{s})\right\}_1 &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_3\right)\\
&\qquad \times \left(\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{r},\\
\left\{x_B^{(m+1)}(\mathbf{s})\right\}_2 &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_3\right)\\
&\qquad \times \left(\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{r},\\
\left\{x_B^{(m+1)}(\mathbf{s})\right\}_3 &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\left(\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_3\right)\right.\\
&\qquad \times\left(\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_3\right) + \left(\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_2 + \frac{1}{2}\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_3\right)\\
&\qquad \left.\times\left(\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_1 + \frac{1}{2}\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_3\right)\right) \mathrm{d}\mathbf{r},
\end{aligned}$$

where

$$\left\{\mathbf{z}_A^{(m)}(\mathbf{r})\right\}_i = \frac{\left\{\mathbf{x}_A^{(m)}(\mathbf{r})\right\}_i \left\{\mathbf{V}\mathbf{y}_B^{(m)}(\mathbf{s})\right\}_i}{(\mathbf{x}_A^{(m)}(\mathbf{r}))'\mathbf{V}\mathbf{y}_B^{(m)}(\mathbf{r})},$$

$$\left\{\mathbf{z}_B^{(m)}(\mathbf{r})\right\}_i = \frac{\left\{\mathbf{y}_B^{(m)}(\mathbf{r})\right\}_i \left\{\mathbf{W}'\mathbf{x}_A^{(m)}(\mathbf{s})\right\}_i}{(\mathbf{y}_B^{(m)}(\mathbf{r}))'\mathbf{W}'\mathbf{x}_A^{(m)}(\mathbf{r})}.$$

Analagous equations may be obtained for females by replacing $\{\mathbf{x}_j^{(m+1)}\}_i$ on the left hand sides by $\{\mathbf{y}_j^{(m+1)}\}_i$ for $i = 1, 2, 3$ and $j = A, B$ and by replacing $p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})$ on the right hand sides by $p_{\mathrm{F}}(\mathbf{s}-\mathbf{r})$.

Suppose initially only the genes A_1 and B_1 are present, and gene A_2 is introduced. The linearised equations in the forward front relating to the heterozygote A_1A_3 for males and females are

$$\begin{aligned}
\left\{\mathbf{x}_A^{(m+1)}(\mathbf{s})\right\}_3 &= \int\limits_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\frac{v_{31}}{2v_{11}}\left\{\mathbf{x}_A^{(m)}(\mathbf{r})\right\}_3 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{s},\\
\left\{\mathbf{y}_A^{(m+1)}(\mathbf{s})\right\}_3 &= \int\limits_{\mathbb{R}^N} p_{\mathrm{F}}(\mathbf{s}-\mathbf{r})\left(\frac{v_{31}}{2v_{11}}\left\{\mathbf{x}_A^{(m)}(\mathbf{r})\right\}_3 + \frac{1}{2}\left\{\mathbf{y}_A^{(m)}(\mathbf{r})\right\}_3\right) \mathrm{d}\mathbf{s}.
\end{aligned} \tag{24}$$

In this case the matrix $\mathbf{A}(\lambda)$ from Section 2 is given by

$$\mathbf{A}(\lambda) = \frac{1}{2v_{11}}\begin{pmatrix} v_{31}P_{\mathrm{M}}(\lambda) & v_{11}P_{\mathrm{M}}(\lambda) \\ v_{31}P_{\mathrm{F}}(\lambda) & v_{11}P_{\mathrm{F}}(\lambda) \end{pmatrix}$$

and hence $\rho(\mathbf{A}(\lambda)) = (1/2v_{11})(v_{31}P_{\mathrm{M}}(\lambda) + v_{11}P_{\mathrm{F}}(\lambda))$. It follows from the general result of Section 2 that the speed of first spread c_A of heterozygote A_1A_2 (and hence of gene A_2 and strategy S_3) is given by

$$c_A = \max\left(0, \inf_{\lambda>0}\left(\frac{\log(v_{31}P_{\mathrm{M}}(\lambda) + v_{11}P_{\mathrm{F}}(\lambda)) - \log(2v_{11})}{\lambda}\right)\right). \tag{25}$$

If initially only the genes A_1 and B_1 are present, and gene B_2 is introduced, the corresponding linearised equations in the forward front corresponding to genotype B_1B_2 are

$$\begin{aligned}
\left\{\mathbf{x}_B^{(m+1)}(\mathbf{s})\right\}_3 &= \int_{\mathbb{R}^N} p_{\mathrm{M}}(\mathbf{s}-\mathbf{r})\left(\frac{1}{2}\left\{\mathbf{x}_B^{(m)}(\mathbf{r})\right\}_3 + \frac{w_{13}}{2w_{11}}\left\{\mathbf{y}_B^{(m)}(\mathbf{r})\right\}_3\right)\mathrm{d}\mathbf{s},\\
\left\{\mathbf{y}_B^{(m+1)}(\mathbf{s})\right\}_3 &= \int_{\mathbb{R}^N} p_{\mathrm{F}}(\mathbf{s}-\mathbf{r})\left(\frac{1}{2}\left\{\mathbf{x}_A^{(m)}(\mathbf{r})\right\}_3 + \frac{w_{13}}{2w_{11}}\left\{\mathbf{y}_B^{(m)}(\mathbf{r})\right\}_3\right)\mathrm{d}\mathbf{s}.
\end{aligned} \tag{26}$$

In this case $\mathbf{A}(\lambda)$ is given by

$$\mathbf{A}(\lambda) = \frac{1}{2w_{11}}\begin{pmatrix} w_{11}P_{\mathrm{M}}(\lambda) & w_{13}P_{\mathrm{M}}(\lambda) \\ w_{11}P_{\mathrm{F}}(\lambda) & w_{13}P_{\mathrm{F}}(\lambda) \end{pmatrix},$$

$\rho(\mathbf{A}(\lambda)) = (1/2w_{11})(w_{13}P_{\mathrm{F}}(\lambda) + w_{11}P_{\mathrm{M}}(\lambda))$, and the speed of first spread c_B of genotype B_1B_2 (and hence of gene B_2 and strategy T_3) is given by

$$c_B = \max\left(0, \inf_{\lambda>0}\left(\frac{\log(w_{31}P_{\mathrm{F}}(\lambda) + w_{11}P_{\mathrm{M}}(\lambda)) - \log(2w_{11})}{\lambda}\right)\right). \tag{27}$$

If both alleles A_2 and B_2 are introduced from outside into a population in which only A_1 and B_1 are present, the linearisation of the system will only be appropriate for the gene which by itself travels faster. Thus if $c_A \geqslant c_B$, the speed of first spread of new genotype A_1A_2, new gene A_2 and new strategy S_3 are given by c_A; and if $c_B \geqslant c_A$ the speed of first spread of new genotype B_1B_2, new gene B_2 and new strategy T_3 are given by c_B. Again when the appropriate point in the non-spatial case is locally stable the speed of first spread in any direction is zero.

7. Conclusion

There are numerous examples in nature where species exhibit gene linked behaviour. Non-spatial sociobiological models have been developed by a number of authors to model competitive situations in animal populations. This includes models for populations competing for food, competition amongst males for females and models for parental investment.

There has been considerable interest in recent years in the development of spatial models. In this paper we have shown how the models can be generalised and extended to include a spatial aspect. Equations may be obtained for the proportions of genotypes in generation *m* at different points in the biological cycle. The complexity of the equations is highly dependent upon the time selected within this cycle. When the models are spatial it is simplest to measure the population structure just after migration. For populations where the strategies and payoffs are not sex dependent, as in the examples of Sections 3 and 4, equations can be obtained for the alleles, since the new generation is in Hardy–Weinberg equilibrium after mating. However when strategies and payoffs do differ between sexes, as is the case for the examples of Sections 5 and 6, it is necessary to work with the genotypes.

We have developed a saddle point method which can be used to obtain the speed of first spread in discrete time spatial models of biological system. It has been used previously only in order to obtain results on the speed of first spread in simple models of genetics and games.

In this paper we have demonstrated the power of the saddle point method when applied to much more complex situations. In sociobiology the strategies are linked to the genes or genotypes. When a new gene is introduced into a population, the associated strategy (or strategies) will also be introduced. The saddle point method enables us to obtain the speed of first spread of a new strategy through a population. Zero speed of spread in the spatial system is linked to local stability in the non-spatial system.

For simplicity of exposition, we have assumed throughout this paper that the migration densities do not depend on the genotypes. It is of course possible to remove this restriction and still obtain the speed of first spread.

The technique is clearly applicable to a wide range of sociobiological models. This paper demonstrates its usefulness via several models of importance and interest in this area.

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