



## Optimal behaviour of honey bees based on imitation at fixed densities

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**Abstract:** The paper deals with two bee species collecting nectar from two plant species. It is assumed that the nectar stock is reduced but not exhausted by the nectar collection, each individual's pay-off depends linearly on its own foraging strategy (i.e., on the probability of a visit to a plant species) and on the average strategies of both species. For the corresponding matrix game model, it is shown that evolutionary stability of a totally mixed equilibrium foraging strategy pair is only determined by the efficiency parameters of nectar collection. The latter parameters depend on morphological characteristics of all involved species, determined by the long-term evolutionary processes. The evolutionarily stable foraging strategy is locally asymptotically stable with respect to the corresponding replicator dynamics.

### 1. Introduction

One of the best known examples of optimal foraging theory is the collection of nectar by bees (Krebs and Davies 1993, Heinrich 1979). With respect to nectar production, there are only two basic types of plants. One type secretes a certain mass of nectar in a well-defined period of the day, while the second one produces nectar continuously (Heinrich 1979). In this paper, we will deal only with plant species that have continuous nectar production. Let us suppose that flowers of several plant species contain nectar, and different bee species may collect nectar from the flowers that are in bloom. Different bee species will have different nectar collecting abilities which depend on their own morphological properties and on those of the flowers. Optimal foraging theory states that each bee species uses nectar collection strategies that guarantee the highest possible benefits, i.e., highest fitness. However, in the situation under consideration, the nectar mass collected by each species does not only depend on its own collecting strategy but also on the other species' strategies, if the nectar mass is decreased by collection. This is then a typical game-theoretical conflict where the pay-off

of each individual does not only depend on his own strategy choice but also on the behaviour of other individuals.

Although the usual biological interpretations of game theoretical conflicts are based on pair-wise interactions, in foraging theory we suppose that the competition is indirect; namely, we ignore pair-wise conflicts between bees, since this kind of interaction is rare. In our case, the individual is thought of as interacting with the average strategies of the species. In evolutionary game theory, this situation is known as "playing the field" (Maynard Smith 1982).

In the pollinator interactions, there are four different time scales during which the system changes. We order these from fastest to slowest. The first one is the time scale of foraging by bees, optimising their fitness during the time period of the order of a day, that is, in a period much shorter than the reproduction period of bees. In this time scale, only the foraging strategies may change, while the density of plants and that of bees remain fixed. The second time scale is the reproduction scale of bees. These two time scales are both fast in comparison with the third one, the time scale of reproduction of plants. This is the eco-

logical time scale in which the evolutionary parameters of the system still remain constant, but the respective densities of the bees and of the plants may change. The fourth time scale is the co-evolutionary scale where the parameters of pollination (e.g., the average number of flowers of a plant, the mass of nectar produced, and the morphology of flowers and bees) may change.

The main aim of this paper is to build up a game-theoretical model for the multi-species foraging problem in which there are two species of bees that visit two plant species for nectar. We will study only the fastest time scale, when only the foraging strategies of bees change. We will show that, in game-theoretic terms, the optimal foraging strategies provide a two-species ESS. We also take into account that during the day the foraging strategies may change according to the actual nectar stock. This change will be modelled in terms of a dynamic system. Specifically, we apply the replicator dynamics (see e.g., Hofbauer and Sigmund 1998) to describe this time variation in foraging strategies. In our approach, the “replication” is actually motivated through imitation of the best foraging strategy (see Weibull 1995 and Section 3 below) given the current species average strategies rather than through a reproduction process. The model presented here does not consider spatial processes.

## 2. A game model for nectar collecting with continuous nectar production

### 2.1. Linear model

Let us consider honey and bumble bees collecting nectar from two plant populations that are in bloom. For plant species 1 and 2, respectively, let us denote by  $n_1$  and  $n_2$  the nectar mass continuously produced in a unit of time by a flower; by  $m_1$  and  $m_2$  the number of flowers; and finally, by  $N_1$  and  $N_2$  the number of plants of species 1 and 2, respectively. Thus, plant species 1 and 2 secrete nectar mass  $N_1n_1m_1$  and  $N_2n_2m_2$ , respectively in one time unit.

Nectar collection and pollination is a co-evolutionarily determined process. For instance, the morphology of flowers and bees together determine not only the mass of the collected nectar but also the pollination of plants (see e.g., Peleg et al. 1992). On the morphology of plants and bees also depends the cost of extracting nectar. Let us denote by  $c_{11}$  and  $c_{12}$  the cost per unit of time for honey bees to collect nectar from flowers of species 1 and 2, and similarly by  $c_{21}$  and  $c_{22}$  the corresponding costs for bumble bees. In reality, these costs also depend on the location of the plants and of the colony of bees, on the densities of plants and bees, on the morphological properties of flowers and bees, and so on. These dependences are not taken

into account. From our study, it will turn out that the only role costs play is in the existence of a totally mixed equilibrium (i.e., when both species of bees visit both plant species), but they have no effect on the dynamical and stability properties of the nectar foraging strategies. Moreover, the morphology of plants and bees also determines the success of nectar collection. Let  $h_{11}$  and  $h_{12}$  be the efficiency of nectar collection by a honey bee, from the stock of plant species 1 and 2, respectively, and define  $h_{21}$  and  $h_{22}$  similarly for bumble bees. Moreover, let  $a_{11}$  and  $a_{12}$  be the rate of successful pollination resulting from a honey bee and bumble bee, respectively visiting a plant of species 1, and define  $a_{21}$  and  $a_{22}$  similarly for a plant of species 2.

In reality, a bee can exhaust the nectar stock of the visited flowers. The flower needs a time to fill up its nectar stock. Moreover, a bee, in general, does not go to all flowers of a visited plant. Usually, if a bee finds nectar in the first or second visited flower then it goes on, visiting further (usually not all) flowers of the same plant (Pyke 1979). For simplicity, we do not build all these factors into the model, and also neglect spatial positions of plants, etc.

Finally, denote by  $M_1$  and  $M_2$  the number of honey and bumble bees, respectively. The strategy of the bees is the proportion of time they spend visiting the different plant species during a day. Denote by  $p_1$  and  $p_2$  the probability of a visit by honey bees to a plant of species 1 and 2, respectively, and put  $\mathbf{p} = (p_1, p_2)$ . Similarly, define  $q_1$ ,  $q_2$  and  $\mathbf{q} = (q_1, q_2)$  for the bumble bees. We assume that all bees visit plants (i.e.,  $p_1 + p_2 = 1 = q_1 + q_2$ ).

First, let us calculate the pay-offs to bees. Fix the densities of plants and bees. Suppose that the individual plants in each species are identical, implying that the nectar in each flower in a given plant species has the same mass. Moreover, the bees reduce the mass of nectar in the flowers. Using the above notation, the nectar stock of plants 1 and 2, respectively is

$$S_1(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M}) = N_1n_1m_1(1 - M_1p_1h_{11} - M_2q_1h_{21}),$$

$$S_2(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M}) = N_2n_2m_2(1 - M_1p_2h_{12} - M_2q_2h_{22}).$$

Since the nectar collecting strategies of the bees depend on the actual nectar stocks, as a result, the nectar stocks also depend on each other. Of course, both stocks must be non negative. We can guarantee this by assuming there are enough plants in both species (e.g., if both bee species visit only one plant species, assume they cannot exhaust the nectar stock which then always remains positive). Observe that the nectar stock depends linearly on the densities and on the strategy choice of bees.

Now let us calculate in this situation the nectar pay-off to an individual honey bee using strategy  $\underline{p}$ , while the average strategy of honey bees is  $\underline{p}$  and that of bumble bees is  $\underline{q}$ . Under the assumption that the populations are large enough, the expected pay-off to this individual is

$$\begin{aligned} H_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = & \underline{p}_1 h_{11} S_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) + \underline{p}_2 h_{12} S_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) - c_{11} \underline{p}_1 - c_{12} \underline{p}_2 = \\ & \underline{p}_1 h_{11} N_1 n_1 m_1 (1 - M_1 p_1 h_{11} - M_2 q_1 h_{21}) + \\ & \underline{p}_2 h_{12} N_2 n_2 m_2 (1 - M_1 p_2 h_{12} - M_2 q_2 h_{22}) - c_{11} \underline{p}_1 - c_{12} \underline{p}_2 . \end{aligned}$$

Likewise, the nectar pay-off to an individual bumble bee using strategy  $\underline{q}$  is

$$\begin{aligned} H_2(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = & \underline{q}_1 h_{21} S_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) + \underline{q}_2 h_{22} S_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) - c_{21} \underline{q}_1 - c_{22} \underline{q}_2 = \\ & \underline{q}_1 h_{21} N_1 n_1 m_1 (1 - M_1 p_1 h_{11} - M_2 q_1 h_{21}) + \\ & \underline{q}_2 h_{22} N_2 n_2 m_2 (1 - M_1 p_2 h_{12} - M_2 q_2 h_{22}) - c_{21} \underline{q}_1 - c_{22} \underline{q}_2 . \end{aligned}$$

**Remark 1.** Let us observe that  $h_{ij}$  could also be regarded as strategies, but in this paper we suppose that  $h_{ij}$  are fixed. That is, they cannot be changed either by bees, or the plants. This is a reasonable assumption if we do not consider the effect of long-term co-evolution, only the short-term ecological optimisation is studied.

**Remark 2.** In spite of the fact that we do not consider the change in plant densities in this paper, our model also gives the pay-offs to plants due to interactions with bees. Specifically, let  $k_1$  and  $k_2$  be the costs of nectar production for a plant of species 1 and 2, respectively. Then the corresponding pay-offs are

$$\Phi_1(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = a_{11} M_1 p_1 + a_{12} M_2 q_1 - k_1 N_1 n_1 m_1,$$

$$\Phi_2(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = a_{21} M_1 p_2 + a_{22} M_2 q_1 - k_2 N_2 n_2 m_2.$$

Of course, to model changes to plant densities, we also need other fitness factors of a plant that do not depend on the pollination process (e.g., density dependent competition between plants).

## 2.2. Foraging game

In this section, we introduce a game that describes the above conflicts between bees. For this purpose, we introduced the following pay-off matrices:

$$\mathbf{A}(\mathbf{N}, \mathbf{M}) := \begin{pmatrix} N_1 n_1 m_1 h_{11} (1 - M_1 h_{11}) - c_{11} & N_1 n_1 m_1 h_{11} - c_{11} \\ N_2 n_2 m_2 h_{12} - c_{12} & N_2 n_2 m_2 h_{12} (1 - M_1 h_{12}) - c_{12} \end{pmatrix}$$

$$\mathbf{B}(\mathbf{N}, \mathbf{M}) := \begin{pmatrix} -N_1 n_1 m_1 M_2 h_{11} h_{21} & 0 \\ 0 & -N_2 n_2 m_2 M_2 h_{12} h_{22} \end{pmatrix}$$

$$\mathbf{C}(\mathbf{N}, \mathbf{M}) := \begin{pmatrix} -N_1 n_1 m_1 M_1 h_{11} h_{21} & 0 \\ 0 & -N_2 n_2 m_2 M_1 h_{12} h_{22} \end{pmatrix}$$

$$\mathbf{D}(\mathbf{N}, \mathbf{M}) := \begin{pmatrix} N_1 n_1 m_1 h_{21} (1 - M_2 h_{21}) - c_{12} & N_1 n_1 m_1 h_{21} - c_{12} \\ N_2 n_2 m_2 h_{22} - c_{22} & N_2 n_2 m_2 h_{22} (1 - M_2 h_{22}) - c_{22} \end{pmatrix}$$

If the honey bees use average strategy  $\underline{p}$  and bumble bees use  $\underline{q}$ , the average pay-off of an individual honey bee is given in matrix form by

$$V(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = \underline{p} \mathbf{A}(\mathbf{N}, \mathbf{M}) \underline{p} + \underline{p} \mathbf{B}(\mathbf{N}, \mathbf{M}) \underline{q}$$

Similarly,

$$W(\underline{p}, \underline{q}, \mathbf{N}, \mathbf{M}) = \underline{q} \mathbf{C}(\mathbf{N}, \mathbf{M}) \underline{p} + \underline{q} \mathbf{D}(\mathbf{N}, \mathbf{M}) \underline{q}$$

is the average pay-off to a bumble bee.

It is well-known, and also intuitively clear, that in the totally mixed equilibrium, the pay-offs of bees coming from different plant species must be equal, but the pay-offs for different bee species can be different. Indeed, if for a particular bee one of the plant species gives more nectar mass than the other one, this bee will increase its own frequency of visiting the better performing species. Thus, the totally mixed equilibrium satisfies the following equations.

$$\begin{aligned} h_{11} N_1 n_1 m_1 (1 - M_1 p_1 h_{11} - M_2 q_1 h_{21}) - c_{11} = \\ h_{12} N_2 n_2 m_2 (1 - M_1 p_2 h_{12} - M_2 q_2 h_{22}) - c_{12} , \end{aligned}$$

$$\begin{aligned} h_{21} N_1 n_1 m_1 (1 - M_1 p_1 h_{11} - M_2 q_1 h_{21}) - c_{21} = \\ h_{22} N_2 n_2 m_2 (1 - M_1 p_2 h_{12} - M_2 q_2 h_{22}) - c_{22} , \end{aligned}$$

$$p_1 + p_2 = 1 , \text{ and}$$

$$q_1 + q_2 = 1 .$$

In the following, we will suppose that the parameters and the densities are such that there exists a unique totally mixed equilibrium. The biological conditions behind this assumption are that the nectar mass must be greater than the cost of nectar collection, and the number of bees is much less than the number of the flowers.

Notice that, using these four equations that need to be satisfied for a totally mixed equilibrium point, only the pay-offs guaranteed by different plants are equal for each bee species, but the nectar stock may be different in different plant species. To see this more clearly, the first two equations can be rewritten as follows.

$$h_{11} S_1(\underline{p}^*, \underline{q}^*, \mathbf{N}, \mathbf{M}) - c_{11} = h_{12} S_2(\underline{p}^*, \underline{q}^*, \mathbf{N}, \mathbf{M}) - c_{12},$$

$$h_{21}S_1(\mathbf{p}^*, \mathbf{q}^*, \mathbf{N}, \mathbf{M}) - c_{21} = h_{22}S_2(\mathbf{p}^*, \mathbf{q}^*, \mathbf{N}, \mathbf{M}) - c_{22}.$$

Observe that there is no reason to expect that the nectar stocks of the plant species are equal at equilibrium.

### 2.3 Evolutionary stability of the equilibrium

In evolutionary game theory, stability of the equilibrium is a central notion. From the ecological point of view, it is also an important problem as to whether the equilibrium is stable or not. The main question to answer is what can happen if a small part of the population changes from the equilibrium strategy. One possibility is that the changers get higher pay-offs implying that the equilibrium will not be maintained. Another one is that the changers have less fitness and the equilibrium is re-established. In the latter case, there is an evolutionary stable equilibrium. It is not so clear what happens if changers in one bee species get a higher pay-off and those in the other a lower. To answer this question, we will say an equilibrium is evolutionarily stable if it satisfies the two-species ESS concept of Cressman (1996).

As mentioned in the Introduction, we only consider the short-time scale problem in which the densities do not change, only the strategies of the bees as they maximise their own fitness. That is, we fix all parameters, except the strategies of bees. We will say a totally mixed  $(\mathbf{p}^*, \mathbf{q}^*)$  is a two-species ESS (see Cressman, 1996) if at least one of the following two inequalities holds

$$\mathbf{p}^* \mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{p}^* \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* > \mathbf{p} \mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{p} \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{p}^*,$$

or

$$\mathbf{q}^* \mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{q}^* \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}^* > \mathbf{q} \mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{q} \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}^*.$$

for all other  $(p, q)$ . The intuitive meaning of this definition is that the changer will be worse off than the resident in at least one species.

Based on Appendix A1, an easy calculation shows that, if there exists a totally mixed equilibrium and  $h_{11}h_{22} \neq h_{12}h_{21}$ , this equilibrium is automatically evolutionarily stable. We discuss the biological relevance of this inequality in the final section. First, the following section shows that this equilibrium is stable from dynamic point of view, as well.

### 3. Optimal nectar collecting dynamics based on imitation at fixed densities

The foraging strategies of bees is not constant, it changes depending on the actual nectar sources. It is well-

known that honey bees give information to each other by “dancing” (Von Frisch 1967). This appears to be a form of information exchange that encourages others to imitate the foraging behaviour of the dancer. The intensity and the length of dance of honey bees are proportional to the nectar stock. If we suppose that this dependence is linear, the imitation dynamic for the average strategy of a colony of honey bees and bumble bees, respectively, can be modelled by the well-known replicator dynamics

$$\begin{aligned} \dot{p}_i &= p_i [V_i(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M}) - V(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M})] \\ \dot{q}_i &= q_i [W_i(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M}) - W(\mathbf{p}, \mathbf{q}, \mathbf{N}, \mathbf{M})] \end{aligned} \quad (1)$$

where  $V_i$  and  $W_i$  are the average pay-offs to honey bee and bumble bee individuals, respectively, using the  $i$ -th pure strategy. Observe that, according to this dynamics, the frequency of the  $i$ -th pure strategy (collecting nectar only from one plant species) will increase, if it gives higher pay-off than the average.

With all densities fixed in our case, the dynamics (1) has the following concrete form

$$\begin{aligned} \dot{p}_1 &= p_1(\mathbf{e}_1 - \mathbf{p}) [\mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p} - \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{q}] \\ \dot{p}_2 &= p_2(\mathbf{e}_2 - \mathbf{p}) [\mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p} - \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{q}] \\ \dot{q}_1 &= q_1(\mathbf{e}_1 - \mathbf{q}) [\mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p} - \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}] \\ \dot{q}_2 &= q_2(\mathbf{e}_2 - \mathbf{q}) [\mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p} - \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}] \end{aligned} \quad (2)$$

where  $\mathbf{e}_i$  denotes the  $i$ -th canonical basic vector. Obviously, the totally mixed equilibrium of the game is also a rest point of the dynamics (2). Using the linearization method (see Appendix A2), this unique interior equilibrium is locally asymptotically stable if  $h_{11}h_{22} \neq h_{12}h_{21}$ . Since this condition is exactly the same as that of the two-species ESS, we conclude optimal foraging behaviour is equivalent to an evolutionarily stable strategy.

### 4. Conclusion

In general, if more than one species compete for more than one resource, their foraging strategies have effects on each other if the resource can be exhausted. This kind of conflict can be modelled in game theoretical terms. In this paper, we introduced a game model for the nectar collection/pollination problem. We consider the simplest case, when the pay-offs of bees linearly depend on the average strategies of bees. In this case, the well-known matrix game model can be used. Under this linearity assumption, we proved that if a unique totally mixed equilibrium strategy exists, then it is evolutionarily stable if there are mor-

phological differences between the different species of bees and/or plants. Such morphological differences imply that the nectar collecting efficiency is different for honey bees as compared to bumble bees and so  $h_{11}h_{22} \neq h_{12}h_{21}$ . We emphasize that the stability of the short-time foraging equilibrium depends only on morphological characteristics determined by the long-term co-evolutionary process.

Moreover, we also show that the same condition also guarantees that the totally mixed equilibrium strategy-pair is locally asymptotically stable for the imitation based replicator dynamics. The mixed equilibrium strategies, in principle, can be realized in two ways. One is that individuals play the corresponding mixed strategies. More often, however, mixed strategies are realized as distributions of pure strategies used at the same time by individuals of the population (Heinrich 1979).

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**Appendix**

**A1.** For the convenience of the reader, we give an equivalent reformulation of a totally mixed two-species ESS (Cressman 1992).  $(\mathbf{p}^*, \mathbf{q}^*)$  is a two-species ESS if for all other  $(\mathbf{p}, \mathbf{q})$  the following five conditions are satisfied:

(i)  $\mathbf{p}^* \mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{p}^* \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{q}^* \geq \mathbf{p} \mathbf{A}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{p} \mathbf{B}(\mathbf{N}, \mathbf{M}) \mathbf{q}^*$

(ii)  $\mathbf{q}^* \mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{q}^* \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}^* \geq \mathbf{q} \mathbf{C}(\mathbf{N}, \mathbf{M}) \mathbf{p}^* + \mathbf{q} \mathbf{D}(\mathbf{N}, \mathbf{M}) \mathbf{q}^*$

(iii)  $(\mathbf{p} - \mathbf{p}^*) \mathbf{A}(\mathbf{N}, \mathbf{M}) (\mathbf{p} - \mathbf{p}^*) < 0$

(iv)  $(\mathbf{q} - \mathbf{q}^*) \mathbf{D}(\mathbf{N}, \mathbf{M}) (\mathbf{q} - \mathbf{q}^*) < 0$

(v) Either  $(\mathbf{p} - \mathbf{p}^*) \mathbf{B}(\mathbf{N}, \mathbf{M}) (\mathbf{q} - \mathbf{q}^*) < 0$  and  $(\mathbf{q} - \mathbf{q}^*) \mathbf{C}(\mathbf{N}, \mathbf{M}) (\mathbf{p} - \mathbf{p}^*) < 0$

or

$[(\mathbf{p} - \mathbf{p}^*) \mathbf{A}(\mathbf{N}, \mathbf{M}) (\mathbf{p} - \mathbf{p}^*)] [(\mathbf{q} - \mathbf{q}^*) \mathbf{D}(\mathbf{N}, \mathbf{M}) (\mathbf{q} - \mathbf{q}^*)] > [(\mathbf{p} - \mathbf{p}^*) \mathbf{B}(\mathbf{N}, \mathbf{M}) (\mathbf{q} - \mathbf{q}^*)] [(\mathbf{q} - \mathbf{q}^*) \mathbf{C}(\mathbf{N}, \mathbf{M}) (\mathbf{p} - \mathbf{p}^*)]$

**A2.** Since  $p_2 = 1 - p_1$  and  $q_2 = 1 - q_1$ , the dynamics (2) becomes the two-dimensional system

$$\begin{aligned} \dot{p}_1 &= p_1 \left[ \begin{pmatrix} 1 \\ 0 \end{pmatrix}^T - \begin{pmatrix} p_1 \\ 1-p_1 \end{pmatrix}^T \right] \left[ \mathbf{A}(\mathbf{N}, \mathbf{M}) \begin{pmatrix} p_1 \\ 1-p_1 \end{pmatrix} - \mathbf{B}(\mathbf{N}, \mathbf{M}) \begin{pmatrix} q_1 \\ 1-q_1 \end{pmatrix} \right] \\ \dot{q}_1 &= q_1 \left[ \begin{pmatrix} 1 \\ 0 \end{pmatrix}^T - \begin{pmatrix} p_1 \\ 1-p_1 \end{pmatrix}^T \right] \left[ \mathbf{C}(\mathbf{N}, \mathbf{M}) \begin{pmatrix} p_1 \\ 1-p_1 \end{pmatrix} - \mathbf{D}(\mathbf{N}, \mathbf{M}) \begin{pmatrix} q_1 \\ 1-q_1 \end{pmatrix} \right] \end{aligned}$$

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This takes the following concrete form

$$\begin{aligned} \dot{p}_1 &= p_1(1-p_1) \left[ h_{12}h_{22} M_2 N_2 n_2 m_2 + h_{12}^2 M_1 N_2 n_2 m_2 + h_{11} N_1 n_1 m_1 - c_{11} - h_{12} N_2 n_2 m_2 + c_{12} \right. \\ &\quad \left. - M_1 (h_{11}^2 N_1 n_1 m_1 + h_{12}^2 N_2 n_2 m_2) p_1 - M_2 (h_{11} h_{21} N_1 n_1 m_1 + h_{12} h_{22} N_2 n_2 m_2) q_1 \right] \end{aligned}$$

$$\begin{aligned} \dot{q}_1 &= q_1(1-q_1) \left[ h_{12}h_{22} M_1 N_2 n_2 m_2 + h_{22}^2 M_2 N_2 n_2 m_2 + h_{21} N_1 n_1 m_1 - c_{21} - h_{22} N_2 n_2 m_2 + c_{22} \right. \\ &\quad \left. - M_1 (h_{11} h_{21} N_1 n_1 m_1 + h_{12} h_{22} N_2 n_2 m_2) p_1 - M_2 (h_{21}^2 N_1 n_1 m_1 + h_{22}^2 N_2 n_2 m_2) q_1 \right] \end{aligned}$$

There are several equilibria where  $p_1 = 0$  or  $p_1 = 1$ ,  $q_1 = 0$  or  $q_1 = 1$ , but we are only interested in a totally mixed equilibrium  $(\mathbf{p}^*, \mathbf{q}^*)$ . This can be found by setting the two expressions in the square brackets above to zero and solving the resultant linear equations for  $p_1$  and  $q_1$ . We assume there is a unique solution with  $0 < p_1 < 1$  and  $0 < q_1 < 1$ . When this solution is substituted into the Jacobian at  $(\mathbf{p}^*, \mathbf{q}^*)$ , we find

$$\mathbf{J}(\mathbf{p}^*, \mathbf{q}^*) = \begin{pmatrix} -M_1 (h_{11}^2 N_1 n_1 m_1 + h_{12}^2 N_2 n_2 m_2) (1-p_1^*) p_1^* & -M_2 (h_{11} h_{21} N_1 n_1 m_1 + h_{12} h_{22} N_2 n_2 m_2) (1-p_1^*) p_1^* \\ -M_1 (h_{11} h_{21} N_1 n_1 m_1 + h_{12} h_{22} N_2 n_2 m_2) (1-q_1^*) q_1^* & -M_2 (h_{21}^2 N_1 n_1 m_1 + h_{22}^2 N_2 n_2 m_2) (1-q_1^*) q_1^* \end{pmatrix}$$

The real parts of both eigenvalues of this Jacobian are negative if

$$\text{tr} \mathbf{J}(\mathbf{p}^*, \mathbf{q}^*) < 0 \text{ and } \text{Det } \mathbf{J}(\mathbf{p}^*, \mathbf{q}^*) > 0.$$

Obviously, the trace of Jacobian is always negative. Moreover, an easy calculation shows that

$$\text{Det } \mathbf{J}(\mathbf{p}^*, \mathbf{q}^*) = M_1 N_1 n_1 m_1 M_2 N_2 n_2 m_2 (h_{11} h_{22} - h_{12} h_{21})^2 > 0.$$

Under the natural assumption that densities  $M_1, N_1, n_1, m_1, M_2, N_2, n_2, m_2$  are positive, the required inequalities for asymptotic stability are always satisfied if  $h_{11} h_{22} \neq h_{12} h_{21}$ .