

# On the non-existence of an optimal migration rate<sup>\*</sup>

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**Abstract.** We show that an optimal migration rate may not exist in a population distributed over an infinite number of individual living sites if empty sites occur. This is the case when the mean number of offspring per individual  $\mu$  is finite. We make the assumption of uniform migration to other sites whose rate is determined by the parent's genotype or the offspring's genotype at a single locus in a diploid hermaphrodite population undergoing random mating. In both cases, for  $\mu$  small enough, any population at fixation would go to extinction. Moreover, in the latter case, for intermediate values of  $\mu$ , the only fixation state that could resist the invasion of any mutant would lead the population to extinction. These are the two conditions for the non-existence of an optimal migration rate. They become less stringent as the cost for migration expressed by a coefficient of selection  $1 - \beta$  becomes larger, that is, closer to 1. The results are obtained assuming that the allele at fixation is either nondominant or dominant. Although the optimal migration rate is the same in both cases when it exists, the optimality properties may differ.

**Key words:** Optimality – ESS – CSS – Migration rate

## 1 Introduction

Hamilton and May (1977) have shown that migration might be favorable even in a saturated environment, and even though offspring who migrate considerably reduce their own chance of surviving. In their model, the environment is partitioned into an infinite number of sites, which are supposed to be constantly occupied by single individuals, one on each site, and the next generation is made of successors randomly chosen among the offspring of the next

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generation present on the different sites. Comparing the fitnesses of individuals using one of two different migration rates in a population, it has been shown that some level of migration corresponds to an unbeatable strategy in Hamilton's (1967) sense. This is what keeps the population away from adopting a sedentary strategy. The fitness of an individual is defined here as the expected number of sites that will be occupied in the next generation by the individual's offspring. Then an unbeatable strategy is defined as a strategy such that any other competing with it in the population cannot have a higher fitness. Therefore any other strategy will have a diminishing frequency in any mixture. In particular, this will be the case when the frequency of this other will be small as occurs initially for mutant strategies. This defines an ESS (evolutionarily stable strategy) in Maynard Smith and Price's (1973) sense.

In a series of papers, Motro (1982a, 1982b, 1983) has made a detailed analysis of Hamilton and May's (1977) model, using exact recurrence equations for gene frequencies, first in haploid populations and then in diploid populations, with migration rate determined either by the parent's genotype or by the offspring's genotype. In these models, migration of offspring to other sites is uniform and the migration rate is genetically determined at a single locus. An optimal migration rate is defined as a rate that can resist the initial invasion of any other rate when at fixation in the population. This corresponds to an ESS in Maynard Smith and Price's (1973) terminology. With the hypothesis of sites being constantly occupied, both the haploid case and the diploid case with migration rate determined by the parent's genotype lead to the same optimal migration rates. In diploid populations with migration rate determined by the offspring's genotype, smaller optimal migration rates are found. Relaxing the assumption of uniform migration of offspring, Comins (1982) has treated the case of a two-dimensional stepping-stone model for haploid populations, where immigrants go to neighbouring sites, and he has shown that to a good approximation the optimal migration rate is independent of the migration pattern.

In most of the above models, all sites are assumed to be occupied. This is the case if there is an infinite number of offspring produced by each individual. Otherwise, the models are only approximate. However some haploid models (Hamilton and May, 1977; Motro, 1982a) have been considered without this assumption. The main effect of allowing empty sites is that the optimal migration rate is smaller than the optimal rate obtained by assuming that all sites are occupied, even though more resources are available to individuals in that case.

Comins, Hamilton and May (1980) have studied a haploid model with  $k$  individuals per site and exogenous extinction of sites. Here the optimal migration rate decreases when the number of mature individuals per site  $k$  increases.

Another way to define an optimal migration rate is to look at the probability of extinction. Karlson and Taylor (1992) have used a branching process model to show that some level of migration is generally needed to keep extinction at furthest reach, by finding the migration rate that minimizes

the extinction probability for the lineage, when sites are subject to exogenous extinction. This optimal rate increases when the number of offspring per individual increases and when the probability of surviving migration increases.

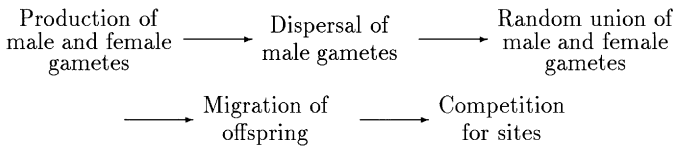
Our work deals with models of the same kind as those of Motro (1982b, 1983) for diploid populations, but we admit the possibility of sites becoming empty. Such models can be viewed as generalizations of the corresponding models with the assumption of a saturated environment. As a matter of fact we get the corresponding results for this case by taking the limit when the mean number of offspring per individual goes to infinity. But we also observe something peculiar, namely, a possible non-existence of an optimal migration rate. This fact has been suggested by Hamilton and May (1977) who have argued, for a particular model, that the only ESS for the migration rate could “imply situations where the population and the species is dangerously liable to extinction” if we do not assume that all sites are constantly occupied, that is when we make the model dependent on the expected number of offspring. Analysis of this question is made in the present paper.

We also make a complete analysis of cases with dominance of an allele determining the migration rate, which have been left over by the previous authors, except Motro (1982a) in his study of haploid populations.

## 2 Formulation of the model

We consider an infinite hermaphrodite diploid population, geographically distributed over an environment partitioned into an infinite number of living sites. Each site can be occupied by at most one single mature individual. Such a situation may model limited local resources. At the beginning of any given generation, every mature individual produces a finite random number of female gametes and a uniformly infinite number of male gametes. While the female gametes stay on the parental site, the male gametes disperse over the entire environment and fertilize at random the female gametes. We suppose that the number of female gametes produced by an individual is a Poisson variable of mean  $\mu$ . Moreover, we suppose that all female gametes are fertilized (though the parameter  $\mu$  can also be interpreted as the mean number of successfully fertilized female gametes). Note that  $\mu$  is also the mean number of successful male gametes per individual. Therefore,  $\mu$  is the mean number of offspring per individual with the convention that every successful gamete counts for half an offspring.

Later on, the offspring either stay on the parental site or migrate uniformly to the other sites, independently of one another. They migrate with a probability determined by their parent's genotype or their own genotype, according to the hypothesis considered. Here the parent is the individual who transmitted the female gamete. The offspring that migrate are called *immigrants* and the offspring that stay on the parental site are called *residents*. The probability to migrate is the *migration rate*.



**Fig. 1.** Life cycle

**Table 1.** Notation for genotypic frequencies and migration rates

Genotype	$A_1A_1$	$A_1A_2$	$A_2A_2$
Migration rate	$\alpha_{11}$	$\alpha_{12}$	$\alpha_{22}$
Frequency	$u$	$v$	$w$

At the end of the given generation, the single parent on every site dies, and there is competition among all offspring present on that site, either residents or immigrants, to occupy the site. Only one of these offspring, called *successor*, will occupy the site at the beginning of the next generation. This successor is assumed to be chosen at random among all competitors present on the site. The entire generation is described by the life cycle of Fig. 1.

Suppose that the migration rate is determined by two alleles,  $A_1$  and  $A_2$ , at a single locus. The migration rates and the genotypic frequencies at the beginning of a generation associated with the three possible genotypes are given in Table 1.

Because migration is risky, we suppose that there is a probability  $1 - \beta$  that an immigrant dies or is lost before competing for a site. This probability is the same for all three genotypes. So there is only a fraction  $\beta$  of all immigrants that will be competing for sites.

We denote by  $u$ ,  $v$  and  $w$  the frequencies, at the beginning of a generation, of the sites occupied by mature individuals of genotype  $A_1A_1$ ,  $A_1A_2$  and  $A_2A_2$ , respectively. As discussed above, sites may be empty, and we denote by  $r = 1 - u - v - w$  their proportion in the whole population. Using this notation, the frequency of allele  $A_1$  is

$$p = \frac{u + v/2}{u + v + w},$$

and the frequency of allele  $A_2$  is

$$q = \frac{w + v/2}{u + v + w}.$$

### 3 Equilibrium points

First let us consider the case where only one allele is present in the population, say  $A_1$ . We want to find an equilibrium for the proportion of sites that are occupied. The following analysis is valid when the migration rate of offspring is determined either by the parent's genotype or by the offspring's genotype. Since we suppose that the number of female gametes produced by any individual is a Poisson variable and that all female gametes are fertilized, the number of offspring competing on every site will be a Poisson variable, due to uniform dispersion of immigrants, and due to statistical independence between the number of residents and the number of immigrants on every site. The proportion of sites occupied by an individual of genotype  $A_1A_1$  from one generation to the next will be

$$u' = u\{1 - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}u]}\} + (1 - u)\{1 - e^{-\mu\beta\alpha_{11}u}\}. \tag{1}$$

Since the function

$$f(u) = u\{1 - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}u]}\} + (1 - u)\{1 - e^{-\mu\beta\alpha_{11}u}\}$$

is increasing and concave for  $0 \leq u \leq 1$ , and satisfies  $f(0) = 0$  and  $f(1) < 1$ , there exists a fixed point  $\tilde{u}$  in the open interval  $(0, 1)$  if and only if  $f'(0) > 1$ . This necessary and sufficient condition is equivalent to

$$\mu\beta\alpha_{11} - e^{-\mu(1-\alpha_{11})} > 0. \tag{2}$$

In this case, the fixed point  $\tilde{u}$  is a globally stable equilibrium point of the recurrence system (1) in the sense that there is convergence to this point from any starting point, as long as no other allele is introduced into the population. Conversely, if (2) fails, the iterates of (1) will converge to 0.

Let us point out that the left hand side of (2) admits an absolute maximum value

$$\beta(\ln \beta + \mu - 1),$$

which is attained when  $\alpha_{11} = 1 + (\ln \beta)/\mu$ . Thus, when  $\ln \beta \leq 1 - \mu$ , the allele  $A_1$  is not viable, whatever may be the migration rate associated with the genotype  $A_1A_1$ , the only equilibrium of (1) being the point  $u = 0$ , which is globally stable. The above condition on the existence of a non-trivial equilibrium point for the frequency of unoccupied site is exactly the same as the one given by Motro (1982a) for a haploid population.

Let us introduce an allele  $A_2$  into the population. Then we get an augmented recurrence system in the form

$$\begin{pmatrix} u' \\ v' \\ w' \\ r' \end{pmatrix} = \begin{pmatrix} P_{uu} & P_{vu} & P_{wu} & P_{ru} \\ P_{uv} & P_{vv} & P_{wv} & P_{rv} \\ P_{uw} & P_{vw} & P_{ww} & P_{rw} \\ P_{ur} & P_{vr} & P_{wr} & P_{rr} \end{pmatrix} \begin{pmatrix} u \\ v \\ w \\ r \end{pmatrix}, \tag{3}$$

where  $P_{ij}$  denotes the probability that the successor of a site previously occupied by an individual of genotype  $i$  is an individual of genotype  $j$ . For convenience, a genotype is represented by its frequency in the subscripts of  $P_{ij}$ . We use the subscript  $r$  to indicate an empty site. The expressions for these transition probabilities are found below.

In the augmented system (3), the point  $(\tilde{u}, 0, 0, 1 - \tilde{u})$  is an equilibrium corresponding to fixation of allele  $A_1$ . Determining conditions for this equilibrium to be locally stable when allele  $A_2$  is introduced in sufficiently small frequency is a way to compare migration strategies adopted by individuals in the population. Then an *optimal strategy* will be defined as a migration rate associated with an allele  $A_1$  in homozygotes  $A_1A_1$  such that  $A_1$ -fixation is locally stable against the invasion of any other allele  $A_2$ , at least to the order of the approximation used.

Since  $r = 1 - u - v - w$ , we will use the vector  $(u, v, w)$  to describe the state of the population.

#### 4 Migration rate determined by the parent's genotype

Let

$$\lambda = \mu\beta(\alpha_{11}u + \alpha_{12}v + \alpha_{22}w)$$

be the mean number of immigrants on a site and

$$\lambda_{11} = \mu\beta(\alpha_{11}up + \alpha_{12}vp/2),$$

$$\lambda_{12} = \mu\beta(\alpha_{11}uq + \alpha_{12}/2 + \alpha_{22}wp),$$

$$\lambda_{22} = \mu\beta(\alpha_{22}wq + \alpha_{12}vq/2),$$

be the mean numbers of immigrants of genotype  $A_1A_1$ ,  $A_1A_2$  and  $A_2A_2$ , respectively, on that site. The transition probabilities in the system (3) can be found in the following way. Let the random variables  $N_{ij}$  ( $i = u, v, w, r$  and  $j = u, v, w$ ) represent the numbers of competitors of type  $j$  on a site previously occupied by an individual of type  $i$ . Under the assumption that the number of female gametes produced by every individual is a Poisson variable of mean  $\mu$  and that these numbers for all individuals are independent, the random variables  $N_{ij}$  are also Poisson variables, independent of one another, whose means are

$$E(N_{iu}) = [\mu(1 - \alpha_{11})p]I_u(i) + [\mu(1 - \alpha_{11})p/2]I_v(i) + \lambda_{11},$$

$$E(N_{iv}) = [\mu(1 - \alpha_{12})q]I_u(i) + [\mu(1 - \alpha_{12})/2]I_v(i) \\ + [\mu(1 - \alpha_{12})p]I_w(i) + \lambda_{12},$$

$$E(N_{iw}) = [\mu(1 - \alpha_{22})q/2]I_v(i) + [\mu(1 - \alpha_{22})q]I_w(i) + \lambda_{22},$$

where

$$I_j(i) = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{if } i \neq j \end{cases}.$$

For  $i = u, v, w, r$ , the probability  $P_{ir}$  is given by

$$P_{ir} = P(N_{iu} + N_{iv} + N_{iw} = 0).$$

We get

$$\begin{aligned} P_{rr} &= e^{-\lambda}, \\ P_{ur} &= e^{-[\mu(1-\alpha_{11})+\lambda]}, \quad P_{vr} = e^{-[\mu(1-\alpha_{12})+\lambda]}, \\ P_{wr} &= e^{-[\mu(1-\alpha_{22})+\lambda]}. \end{aligned}$$

For  $i = u, v, w, r$  and  $j = u, v, w$ , the transition probabilities  $P_{ij}$  are given by

$$\begin{aligned} P_{ij} &= (1 - P_{ir})E\left(\frac{N_{ij}}{N_{iu} + N_{iv} + N_{iw}} \middle| N_{iu} + N_{iv} + N_{iw} > 0\right) \\ &= (1 - P_{ir})\left[\frac{E(N_{ij})}{E(N_{iu} + N_{iv} + N_{iw})}\right], \end{aligned} \tag{4}$$

the second equality being a property of independent Poisson variables (see Appendix A.1). We find

$$\begin{aligned} P_{ru} &= (1 - P_{rr})\frac{\lambda_{11}}{\lambda}, \quad P_{rv} = (1 - P_{rr})\frac{\lambda_{12}}{\lambda}, \quad P_{rw} = (1 - P_{rr})\frac{\lambda_{22}}{\lambda}, \\ P_{uu} &= (1 - P_{ur})\left[\frac{\mu(1 - \alpha_{11})p + \lambda_{11}}{\mu(1 - \alpha_{11}) + \lambda}\right], \\ P_{uv} &= (1 - P_{ur})\left[\frac{\mu(1 - \alpha_{11})q + \lambda_{12}}{\mu(1 - \alpha_{11}) + \lambda}\right], \\ P_{uw} &= (1 - P_{ur})\left[\frac{\lambda_{22}}{\mu(1 - \alpha_{11}) + \lambda}\right], \\ P_{vu} &= (1 - P_{vr})\left[\frac{\mu(1 - \alpha_{12})p/2 + \lambda_{11}}{\mu(1 - \alpha_{12}) + \lambda}\right], \\ P_{vv} &= (1 - P_{vr})\left[\frac{\mu(1 - \alpha_{12})/2 + \lambda_{12}}{\mu(1 - \alpha_{12}) + \lambda}\right], \\ P_{vw} &= (1 - P_{vr})\left[\frac{\mu(1 - \alpha_{12})q/2 + \lambda_{22}}{\mu(1 - \alpha_{12}) + \lambda}\right], \\ P_{wu} &= (1 - P_{wr})\left[\frac{\lambda_{11}}{\mu(1 - \alpha_{22}) + \lambda}\right], \\ P_{wv} &= (1 - P_{wr})\left[\frac{\mu(1 - \alpha_{22})p + \lambda_{12}}{\mu(1 - \alpha_{22}) + \lambda}\right], \\ P_{ww} &= (1 - P_{wr})\left[\frac{\mu(1 - \alpha_{22})q + \lambda_{22}}{\mu(1 - \alpha_{22}) + \lambda}\right]. \end{aligned} \tag{5}$$

We have the following result on local stability of the equilibrium  $(\tilde{u}, 0, 0)$ , which is valid only if allele  $A_1$  is not dominant ( $\alpha_{12} \neq \alpha_{11}$ ). This result is obtained by analyzing the largest eigenvalue of the linear approximation of the recurrence system  $(u', v', w')$  in a neighbourhood of the equilibrium point (see Appendix B.1).

**Result 4.1.** *In the case of no dominance of allele  $A_1$ , the equilibrium point  $(\tilde{u}, 0, 0)$  of the recurrence system  $(u', v', w')$  with the transition probabilities (5) is locally stable if inequality (2) is satisfied, and if*

$$\frac{1}{\alpha_{11}} [1 - g(\alpha_{11}, \alpha_{11})] < \frac{1}{\alpha_{12}} [1 - g(\alpha_{11}, \alpha_{12})], \tag{6}$$

where

$$g(\alpha_{11}, \alpha) = \{1 - e^{-[\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}]}\} \frac{\mu(1-\alpha)}{\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}}$$

and  $\tilde{u}$  is the unique fixed point in  $(0, 1)$  of the recurrence equation (1).

If allele  $A_1$  is dominant ( $\alpha_{12} = \alpha_{11}$ ), we get a degeneracy, the largest eigenvalue of the linear approximation of the recurrence system (3) being equal to one. The local stability of the equilibrium point cannot be decided from linear approximations. A quadratic analysis can be performed, based on a criterion proposed by Lessard and Karlin (1982) presented under more general conditions in Morris, Matessi and Karlin (1987). This criterion, described in Appendix C.1, serves us to prove the following result, in the case of dominance of allele  $A_1$  (see Appendix C.2).

**Result 4.2.** *In the case of dominance of allele  $A_1$ , the equilibrium point  $(\tilde{u}, 0, 0)$  of the recurrence system  $(u', v', w')$  with the transition probabilities (5) is locally stable if inequality (2) is satisfied, and if*

$$\frac{1}{\alpha_{11}} [1 - g(\alpha_{11}, \alpha_{11})] < \frac{1}{\alpha_{22}} [1 - g(\alpha_{11}, \alpha_{22})], \tag{7}$$

where

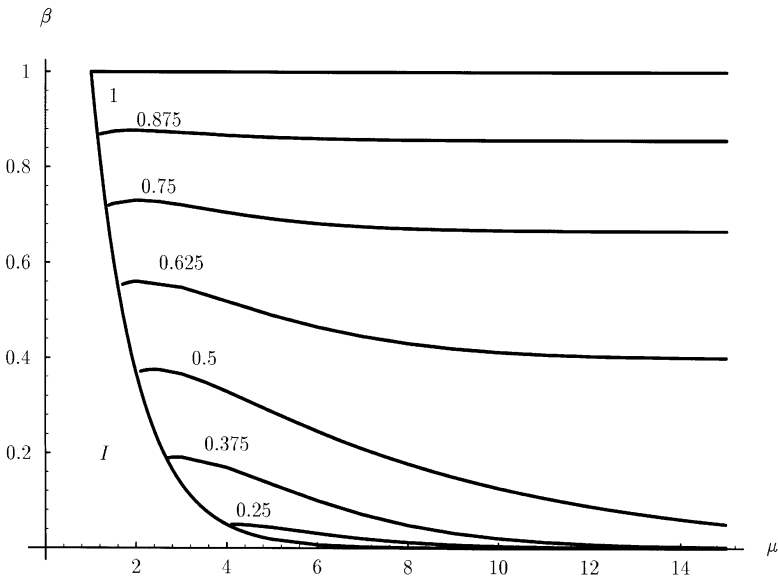
$$g(\alpha_{11}, \alpha) = \{1 - e^{-[\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}]}\} \frac{\mu(1-\alpha)}{\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}}$$

and  $\tilde{u}$  is the unique fixed point in  $(0, 1)$  of the recurrence equation (1).

Note that the above condition for local stability of  $A_1$ -fixation with dominance of  $A_1$  is in the same form as the condition with no dominance of  $A_1$ , except that  $\alpha_{11}$  is now confronted with  $\alpha_{22}$ . Inequalities (6) and (7) have a nice interpretation, which will be presented in the discussion section.

Figure 2 shows numerical results for the optimal migration rate when the migration rate is determined by the parent's genotype. This optimal rate is the value  $\alpha_{11}$  which satisfies inequality (6) (or (7), the dominance case leading to the same optimal rate) for every rate  $\alpha_{12}$  (or  $\alpha_{22}$ , respectively) different from  $\alpha_{11}$ . This figure shows level curves of the optimal rate, as a function of  $\mu$  and  $\beta$ . The region  $I$  represents the situation where inequality (2) is not satisfied for





**Fig. 2.** Optimal migration rate determined by the parent’s genotype. In region *I*, there exists no optimal migration rate

any rate  $\alpha_{11}$  (the cases where  $\ln \beta \leq 1 - \mu$ ), so that allele  $A_1$  is not viable at fixation state. No optimal migration rate can exist in this region.

For any fixed  $\beta > 0$ , the optimal rate converges to a value which is strictly greater than  $\frac{1}{2}$ , as  $\mu$  goes to infinity. Actually it converges to the value

$$\frac{1}{2 - \beta},$$

which is the optimal migration rate given by Motro (1982b) in the case of no vacant site under the assumption of a large number of offspring per site (see Appendix B.1). This is a value also found by Taylor (1988), using an inclusive fitness approach. From Fig. 2, we see that any level curve  $\beta(\mu)$  associated with a fixed optimal rate  $\alpha$  decreases as  $\mu$  increases at least for large enough values of  $\mu$ . As  $\mu$  goes to infinity, the level curve  $\beta(\mu)$  converges to the value  $\beta$  such that  $\alpha = 1/(2 - \beta)$ . This limit case corresponds to the model with all sites being constantly occupied. Moreover the optimal rate for any  $\mu$  finite is always smaller than the optimal rate for  $\mu$  infinite.

**5 Migration rate determined by the offspring’s genotype**

In the case where it is the offspring’s genotype that determines the migration rate, the mean number of immigrants on a site is

$$\lambda = \mu\beta(\alpha_{11}up + \alpha_{11}vp/2 + \alpha_{12}uq + \alpha_{12}v/2 + \alpha_{12}wp + \alpha_{22}vq/2 + \alpha_{22}wq),$$

and the mean numbers of immigrants of genotype  $A_1A_1$ ,  $A_1A_2$  and  $A_2A_2$ , respectively, on that site are

$$\begin{aligned} \lambda_{11} &= \mu\beta(\alpha_{11}up + \alpha_{11}vp/2), \\ \lambda_{12} &= \mu\beta(\alpha_{12}uq + \alpha_{12}v/2 + \alpha_{12}wp), \\ \lambda_{22} &= \mu\beta(\alpha_{22}vq/2 + \alpha_{22}wq). \end{aligned}$$

As in Sect. 4, we calculate the transition probabilities of the recurrence system (3) using the random variables  $N_{ij}$ , whose means, with the migration rate determined by the offspring's genotype, are

$$\begin{aligned} E(N_{iu}) &= [\mu(1 - \alpha_{11})p]I_u(i) + [\mu(1 - \alpha_{11})p/2]I_v(i) + \lambda_{11}, \\ E(N_{iv}) &= [\mu(1 - \alpha_{12})q]I_u(i) + [\mu(1 - \alpha_{12})/2]I_v(i) \\ &\quad + [\mu(1 - \alpha_{12})p]I_w(i) + \lambda_{12}, \\ E(N_{iw}) &= [\mu(1 - \alpha_{22})q/2]I_v(i) + [\mu(1 - \alpha_{22})q]I_w(i) + \lambda_{22}, \end{aligned}$$

where

$$I_j(i) = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{if } i \neq j. \end{cases}$$

Using relation (4), we get

$$\begin{aligned} P_{rr} &= e^{-\lambda}, \\ P_{ur} &= e^{-[\mu(1 - \alpha_{11})p + \mu(1 - \alpha_{12})q + \lambda]}, \\ P_{vr} &= e^{-[\mu(1 - \alpha_{11})p/2 + \mu(1 - \alpha_{12})/2 + \mu(1 - \alpha_{22})q/2 + \lambda]}, \\ P_{wr} &= e^{-[\mu(1 - \alpha_{12})p + \mu(1 - \alpha_{22})q + \lambda]}, \\ P_{uu} &= (1 - P_{ur}) \left[ \frac{\mu(1 - \alpha_{11})p + \lambda_{11}}{\mu(1 - \alpha_{11})p + \mu(1 - \alpha_{12})q + \lambda} \right], \\ P_{uv} &= (1 - P_{ur}) \left[ \frac{\mu(1 - \alpha_{12})q + \lambda_{12}}{\mu(1 - \alpha_{11})p + \mu(1 - \alpha_{12})q + \lambda} \right], \\ P_{uw} &= (1 - P_{ur}) \left[ \frac{\lambda_{22}}{\mu(1 - \alpha_{11})p + \mu(1 - \alpha_{12})q + \lambda} \right], \\ P_{vu} &= (1 - P_{vr}) \left[ \frac{\mu(1 - \alpha_{11})p/2 + \lambda_{11}}{\mu(1 - \alpha_{11})p/2 + \mu(1 - \alpha_{12})/2 + \mu(1 - \alpha_{22})q/2 + \lambda} \right], \\ P_{vv} &= (1 - P_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2 + \lambda_{12}}{\mu(1 - \alpha_{11})p/2 + \mu(1 - \alpha_{12})/2 + \mu(1 - \alpha_{22})q/2 + \lambda} \right], \\ P_{vw} &= (1 - P_{vr}) \left[ \frac{\mu(1 - \alpha_{22})q/2 + \lambda_{22}}{\mu(1 - \alpha_{11})p/2 + \mu(1 - \alpha_{12})/2 + \mu(1 - \alpha_{22})q/2 + \lambda} \right], \end{aligned}$$

$$\begin{aligned}
 P_{wu} &= (1 - P_{wr}) \left[ \frac{\lambda_{11}}{\mu(1 - \alpha_{22})p + \mu(1 - \alpha_{22})q + \lambda} \right], \\
 P_{wv} &= (1 - P_{wr}) \left[ \frac{\mu(1 - \alpha_{12})p + \lambda_{12}}{\mu(1 - \alpha_{22})p + \mu(1 - \alpha_{22})q + \lambda} \right], \\
 P_{ww} &= (1 - P_{wr}) \left[ \frac{\mu(1 - \alpha_{22})q + \lambda_{22}}{\mu(1 - \alpha_{22})p + \mu(1 - \alpha_{22})q + \lambda} \right], \\
 P_{ru} &= (1 - P_{rr}) \frac{\lambda_{11}}{\lambda}, \quad P_{rv} = (1 - P_{rr}) \frac{\lambda_{12}}{\lambda}, \quad P_{rw} = (1 - P_{rr}) \frac{\lambda_{22}}{\lambda}. \tag{8}
 \end{aligned}$$

We suppose first that allele  $A_1$  is not dominant, that is  $\alpha_{12} \neq \alpha_{11}$ . The following result, proven in Appendix B.2, states the condition for  $A_1$ -fixation to be locally stable.

**Result 5.3.** *In the case of no dominance of allele  $A_1$ , the equilibrium point  $(\tilde{u}, 0, 0)$  of the recurrence system  $(u', v', w')$  with the transition probabilities (8) is locally stable if inequality (2) is satisfied, and if*

$$\frac{1}{\alpha_{11}} [1 - G(\alpha_{11}, \alpha_{11})] < \frac{1}{\alpha_{12}} [1 - G(\alpha_{11}, \alpha_{12})], \tag{9}$$

where

$$\begin{aligned}
 G(\alpha_{11}, \alpha) &= \frac{\{1 - e^{-[\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]}\} \mu(1 - \alpha)/2}{\{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}\}} \\
 &+ \frac{\{1 - e^{-[\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha)/2 + \mu\beta\alpha_{11}\tilde{u}]}\} \mu(1 - \alpha)/2}{\{\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha)/2 + \mu\beta\alpha_{11}\tilde{u}\}}
 \end{aligned}$$

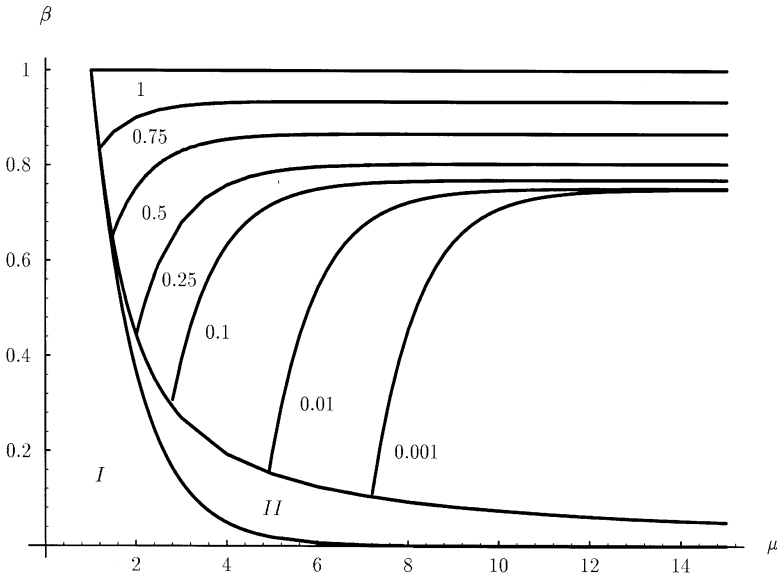
and  $\tilde{u}$  is the unique fixed point in  $(0, 1)$  of the recurrence equation (1).

A necessary condition for inequality (9) to be satisfied for every  $\alpha_{12} \neq \alpha_{11}$  is

$$\left. \frac{\partial}{\partial \alpha} \left\{ \frac{1}{\alpha} [1 - G(\alpha_{11}, \alpha)] \right\} \right|_{\alpha = \alpha_{11}} = 0. \tag{10}$$

This equation has always a solution in  $\alpha_{11}$ , the left hand side of the equation tending to  $-\infty$  as  $\alpha_{11}$  goes to 0, and being positive when  $\alpha_{11} = 1$ . Numerical results indicate that this solution is unique. The numerical values of the optimal rate of migration are presented in Fig. 3. This figure presents some level curves of the optimal migration rate, as a function of  $\mu$  and  $\beta$ , along with two regions where the optimal rate does not exist.

In the region  $I$ , allele  $A_1$  is not viable at fixation; condition (2) is not satisfied for any rate  $\alpha_{11}$ . It coincides with the region  $I$  in Fig. 2 (the situations where  $\ln \beta \leq 1 - \mu$ ). In the region  $II$ , although certain migration rates guarantee the survival of allele  $A_1$  at fixation state, the solution of (10) does not satisfy condition (2). Therefore, in this region, there is no optimal migration rate even if there exists an equilibrium  $\tilde{u} \neq 0$  at fixation state for some  $\alpha_{11}$ .



**Fig. 3.** Optimal migration rate determined by the offspring’s genotype. In regions I and II, there exists no optimal migration rate

In the region where there exists an optimal migration rate, this rate increases with the probability of survival of the immigrants,  $\beta$ , for each  $\mu$  fixed. For small values of  $\beta$ , the optimal rate decreases rapidly to 0 when the mean number of offspring increases. But in all cases, we observe that as  $\mu$  approaches infinity, the optimal migration rate converges to a value which agrees with the rate predicted by Motro (1983), that is

$$\alpha^* = \begin{cases} 0 & \text{if } 0 < \beta \leq \frac{3}{4} \\ \frac{\beta - \frac{3}{4}}{(\beta - \frac{1}{2})(\frac{3}{2} - \beta)} & \text{if } \frac{3}{4} < \beta \leq 1 \end{cases},$$

where the sites are supposed to be constantly occupied (see Appendix B.2). Here the possibility of sites becoming empty leads to an optimal migration rate, if it exists, higher than  $\alpha^*$ . The situation where  $\alpha_{12} = \alpha_{11}$  forces us to take into account the quadratic approximation of the recurrence system  $(u', v', w')$ , the largest eigenvalue of the matrix of the linear approximation of this system being equal to 1. We have the following result (see Appendix C.3).

**Result 5.4.** *In the case of dominance of allele  $A_1$ , the equilibrium point  $(\tilde{u}, 0, 0)$  of the recurrence system  $(u', v', w')$  with the transition probabilities (8) is locally stable if inequality (2) is satisfied, and if*

$$\frac{1}{\alpha_{11}} [1 - H(\alpha_{11}, \alpha_{11})] < \frac{1}{\alpha_{22}} [1 - H(\alpha_{11}, \alpha_{22})], \tag{11}$$

where

$$\begin{aligned}
 H(\alpha_{11}, \alpha) = & \left\{ 1 - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \right\} \frac{\mu(1-\alpha)}{\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \\
 & + \left\{ 1 - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \right\} \left\{ \frac{\mu(1-\alpha_{11})/2}{\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right\}^2 \\
 & - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \left\{ \frac{[\mu(1-\alpha_{11})/2]^2}{\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right\} \\
 & - \left\{ 1 - e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \right\} \left\{ \frac{\mu^2(1-\alpha_{11})(1-\alpha)/4}{[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]^2} \right\} \\
 & + e^{-[\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \left\{ \frac{\mu^2(1-\alpha_{11})(1-\alpha)/4}{\mu(1-\alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right\}
 \end{aligned}$$

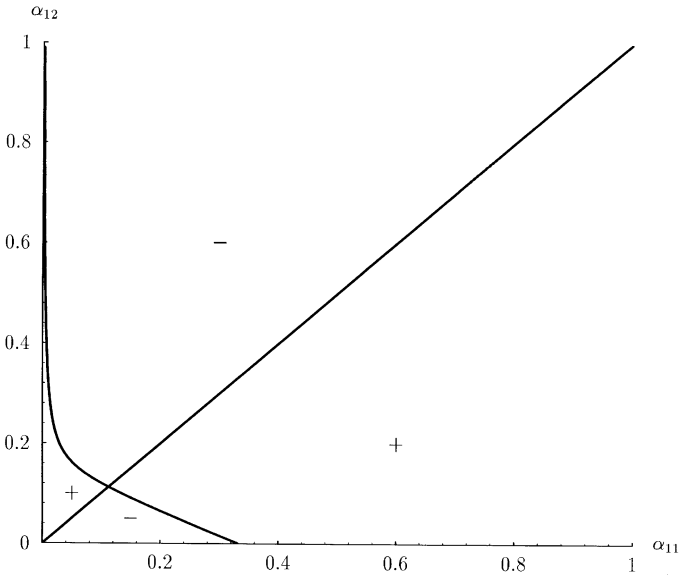
and  $\tilde{u}$  is the unique fixed point in  $(0, 1)$  of the recurrence equation (1).

Although result 5.4 differs from result 5.3, it turns out that the same optimal migration rate prevails if it exists. This can be shown by verifying the equality

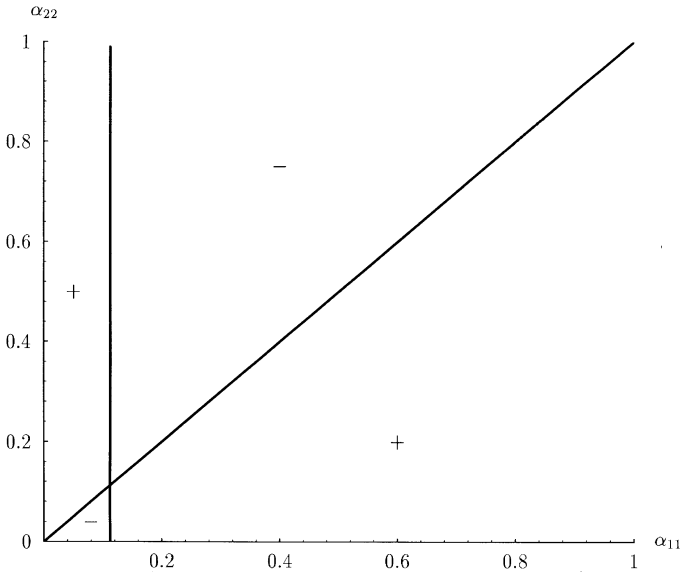
$$\left. \frac{\partial}{\partial \alpha} \left\{ \frac{1}{\alpha} [1 - G(\alpha_{11}, \alpha)] \right\} \right|_{\alpha=\alpha_{11}} = \left. \frac{\partial}{\partial \alpha} \left\{ \frac{1}{\alpha} [1 - H(\alpha_{11}, \alpha)] \right\} \right|_{\alpha=\alpha_{11}}.$$

But there is still a degeneracy in the stability analysis when the population at  $A_1$ -fixation adopts the optimal rate. If we analyse the regions for local stability and for instability of the fixation state according to the resident migration rate and the mutant migration rate, we observe a vertical line delimiting these regions above and below the main diagonal in the case of dominance of allele  $A_1$  (see Fig. 5). The optimal rate must be precisely located at the intersection of this vertical line with the main diagonal. These two lines correspond to the case where local stability is not tractable using a second order approximation (see Appendix C). Therefore, once the population adopts the migration rate at the intersection of these two lines at fixation state, it is not clear whether or not it can be destabilized by a newly arising mutant allele. However, this migration rate is the only candidate to be the optimal rate. Such a degeneracy is not present when allele  $A_1$  is not dominant, as shown in Fig. 4. Here the curves delimiting the regions for local stability and for instability correspond to the case of a first order approximation with a largest eigenvalue equal to 1. To get the results of Figs. 4 and 5, we used the parameters  $\mu = 8$  and  $\beta = 0.77$ , but our conclusions are of general validity.

Note also that if  $\alpha_{11}$  is different from the optimal rate, then the population at  $A_1$ -fixation will be invaded by a wider range of mutant migration rate in the case of dominance of allele  $A_1$  than in the case of no dominance of  $A_1$ . This was not the case in the model of migration rate determined by the parent's genotype since the conditions for local stability are analogous in both cases.



**Fig. 4.** Stability regions for  $A_1$ -fixation with the migration rate determined by the offspring with no dominance of allele  $A_1$ . A plus (+) sign indicates initial invasion of the mutant allele, while a minus (-) sign indicates local stability



**Fig. 5.** Stability regions for  $A_1$ -fixation with the migration rate determined by the offspring with dominance of allele  $A_1$ . A plus (+) sign indicates initial invasion of the mutant allele, while a minus (-) sign indicates local stability

### 6 Discussion

Conditions (6) and (7) for local stability of  $A_1$ -fixation in the case of migration rate determined by the parent's genotype have a nice interpretation. If the population consists only of individuals having migration rate  $\alpha_{11}$ , and if we introduce only one individual having a migration rate  $\alpha$  into the population, then the probability that this individual will lose his site to an offspring that is not his, or that his site will become empty is given by

$$1 - \{1 - e^{-[\mu(1-\alpha) + \mu\beta\alpha_{11}\bar{u}]}\} \frac{\mu(1-\alpha)}{\mu(1-\alpha) + \mu\beta\alpha_{11}\bar{u}},$$

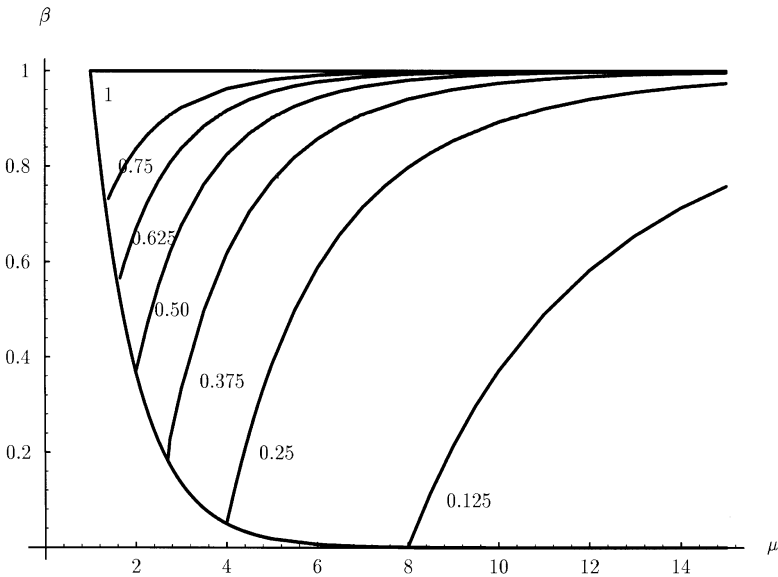
that is, 1 minus the probability that one of his offspring will take over his site in the next generation (see result A.1 with  $X_1$  the number of resident offspring and  $X_2$  the number of immigrant offspring on that site). Moreover, the mean number of sites that will be taken by his immigrant offspring is proportional to  $\alpha$ . Therefore, the ratio

$$\frac{1}{\alpha} \left[ 1 - \{1 - e^{-[\mu(1-\alpha) + \mu\beta\alpha_{11}\bar{u}]}\} \frac{\mu(1-\alpha)}{\mu(1-\alpha) + \mu\beta\alpha_{11}\bar{u}} \right]$$

represents a ratio of lost over gain in terms of sites taken by the individual's offspring. It corresponds to the fitness function used in Hamilton and May's (1977) study on the optimal migration rate. For the sake of his offspring, it is advantageous for an individual to make this ratio as small as possible. Therefore, not only the optimal migration rate makes it impossible for a mutant allele to invade the population, but it also maximizes the mean number of offspring of an individual in the next generation. Conditions (9) and (11) for local stability of  $A_1$ -fixation in the case of migration rate determined by the offspring's genotype might have a similar interpretation, but in such a case it is far less evident.

In the two models studied in the present paper, the non-existence of an optimal migration rate due to extinction of the population at any fixation state (region I in Figs. 2 and 3) has been demonstrated for sufficiently small values of  $\mu$ , the mean number of female gametes produced by an individual, whatever may be the cost of migration expressed by the coefficient of selection  $1 - \beta$ . Such an extinction occurs for smaller values of  $\mu$  when the cost of migration becomes smaller.

In the case of a migration rate determined by the offspring's genotype, there is no optimal migration rate also for intermediate values of  $\mu$  (region II in Fig. 3) since then the only candidate at fixation would lead to extinction of the population. This is the main difference between this case and the case of a migration rate determined by the parent's genotype. Another difference is that the optimal migration rate increases slowly and then rapidly as  $\beta$  increases in the former case while it increases rapidly and then slowly as  $\beta$  increases in the latter case. Also, the optimal migration rate increases for a fixed  $\beta$  when  $\mu$  increases, except for small values of  $\mu$ , in the case of



**Fig. 6.** Migration rate that maximizes the proportion of occupied sites

a migration rate determined by the parent's genotype, while it decreases when  $\mu$  increases in the case of a migration rate determined by the offspring's genotype. In all cases, the optimal migration rate when determined by the offspring's genotype is smaller than the optimal migration rate determined by the parent's genotype.

Note that for parameters  $\mu$  and  $\beta$  in region *II* in Fig. 3, a reduction of the migration rate is favorable, in the sense that a reduced value of  $\alpha_{12}$  compared to  $\alpha_{11}$  will lead to invasion of  $A_1$ -fixation by the mutant allele  $A_2$  at least initially following the introduction of  $A_2$  in small frequency. But it is possible for the population to go extinct after the introduction of a mutant allele  $A_2$ . If, for instance, the homozygote  $A_2A_2$  has a migration rate 0, then the proportion of vacant sites converges to 1. This has been checked numerically. Thus region *II* may lead to quite an unstable situation where the invasion of a mutant allele may cause the extinction of the entire population.

The cases with or without dominance of the allele at fixation lead to the same optimal migration rate. But the nature of optimality is not the same when the migration rate is determined by the offspring's genotype. In the case of no dominance, the optimal migration rate is a continuously stable strategy (CSS) in Eshel's (1983) sense while, in the case of dominance, it is only an evolutionarily stable strategy (ESS) in Maynard Smith and Price's (1973) sense (see Figs. 4 and 5) that satisfies a necessary condition to be a CSS. In the former case, the optimal migration rate at fixation is locally stable against the introduction of any mutant, while in the latter there is a degeneracy in the stability analysis, any mutant being maintained in the population to the order of the approximation.



Figure 6 gives the rate of migration that maximizes the proportion of occupied sites when the population is at fixation. This is the rate of “maximal occupancy” (Hamilton and May, 1977). The proportion of occupied sites can represent the fitness of the population. We observe that for any fixed  $\beta$ , the migration rate at fixation that maximizes this fitness decreases as  $\mu$  increases, and that for any fixed  $\mu$ , it increases as the cost of migration  $1 - \beta$  decreases. Comparing Figs. 6 and 2, we see that this optimal rate determined by the population fitness is smaller than the optimal rate determined by the parent’s genotype, while comparing Figs. 6 and 3, we see that the former is generally higher than the optimal rate determined by the offspring’s genotype, except for large enough values of  $\mu$ . We conclude that the optimal rate determined by the parent’s genotype and by the offspring’s genotype are both suboptimal for the population as a whole as in Hamilton and May (1977) model.

*Acknowledgements.* We thank two anonymous referees for their comments, especially one who has suggested to study the migration rate that optimizes population fitness.

### Appendix A

#### A.1 Proof of Relation 4

**Result A.1.** *If  $X_1$  and  $X_2$  are two independent Poisson random variables, with means  $\lambda_1$  and  $\lambda_2$  respectively, then we have*

$$E\left(\frac{X_1}{X_1 + X_2} \middle| X_1 + X_2 > 0\right) = \frac{E(X_1)}{E(X_1 + X_2)}.$$

*Proof.* The joint distribution of  $X_1$  and  $X_2$ , subject to  $X_1 + X_2 > 0$ , is given by

$$\begin{aligned} P(X_1 = k_1, X_2 = k_2 | X_1 + X_2 > 0) &= \frac{P(X_1 = k_1, X_2 = k_2)}{P(X_1 + X_2 > 0)} \\ &= \left(\frac{1}{1 - e^{-(\lambda_1 + \lambda_2)}}\right) \left(\frac{e^{-\lambda_1} \lambda_1^{k_1}}{k_1!}\right) \left(\frac{e^{-\lambda_2} \lambda_2^{k_2}}{k_2!}\right), \end{aligned}$$

for  $k_1 = 0, 1, \dots, k_2 = 0, 1, \dots$  and  $k_1 + k_2 > 0$ . Thus, we have

$$\begin{aligned} E\left(\frac{X_1}{X_1 + X_2} \middle| X_1 + X_2 > 0\right) &= \left(\frac{1}{1 - e^{-(\lambda_1 + \lambda_2)}}\right) \left(\sum_{k_1=1}^{\infty} \sum_{k_2=0}^{\infty} \frac{k_1}{k_1 + k_2} \left(\frac{e^{-\lambda_1} \lambda_1^{k_1}}{k_1!}\right) \left(\frac{e^{-\lambda_2} \lambda_2^{k_2}}{k_2!}\right)\right) \\ &= \left(\frac{\lambda_1}{1 - e^{-(\lambda_1 + \lambda_2)}}\right) \left(\sum_{k_1=0}^{\infty} \sum_{k_2=0}^{\infty} \frac{1}{k_1 + k_2 + 1} \left(\frac{e^{-\lambda_1} \lambda_1^{k_1}}{k_1!}\right) \left(\frac{e^{-\lambda_2} \lambda_2^{k_2}}{k_2!}\right)\right) \end{aligned}$$

$$\begin{aligned}
 &= \left( \frac{\lambda_1}{1 - e^{-(\lambda_1 + \lambda_2)}} \right) E \left( \frac{1}{X_1 + X_2 + 1} \right) \\
 &= \left( \frac{\lambda_1}{1 - e^{-(\lambda_1 + \lambda_2)}} \right) E \left( \frac{1}{Y + 1} \right),
 \end{aligned}$$

where  $Y$  is a Poisson variable of mean  $\lambda_1 + \lambda_2$ . But then

$$\begin{aligned}
 E \left( \frac{1}{Y + 1} \right) &= \sum_{k=0}^{\infty} \frac{1}{k + 1} \left( \frac{e^{-(\lambda_1 + \lambda_2)} (\lambda_1 + \lambda_2)^k}{k!} \right) \\
 &= \frac{1}{\lambda_1 + \lambda_2} \sum_{k'=1}^{\infty} \frac{e^{-(\lambda_1 + \lambda_2)} (\lambda_1 + \lambda_2)^{k'}}{k'!} \\
 &= \frac{1}{\lambda_1 + \lambda_2} (1 - e^{-(\lambda_1 + \lambda_2)}).
 \end{aligned}$$

Therefore we have

$$\begin{aligned}
 E \left( \frac{X_1}{X_1 + X_2} \middle| X_1 + X_2 > 0 \right) &= \frac{\lambda_1}{\lambda_1 + \lambda_2} \\
 &= \frac{E(X_1)}{E(X_1 + X_2)}. \quad \square
 \end{aligned}$$

## Appendix B

### B.1 Proof of Result 4.1

The linear approximation of  $(u', v', w')$  in a neighborhood of the equilibrium point  $(\tilde{u}, 0, 0)$  is given by

$$\begin{pmatrix} u' - \tilde{u} \\ v' \\ w' \end{pmatrix} \doteq \begin{pmatrix} \frac{\partial u'}{\partial u} & \frac{\partial u'}{\partial v} & \frac{\partial u'}{\partial w} \\ \frac{\partial v'}{\partial u} & \frac{\partial v'}{\partial v} & \frac{\partial v'}{\partial w} \\ \frac{\partial w'}{\partial u} & \frac{\partial w'}{\partial v} & \frac{\partial w'}{\partial w} \end{pmatrix} \begin{pmatrix} u - \tilde{u} \\ v \\ w \end{pmatrix},$$

where the elements of the Jacobian matrix are evaluated at  $(\tilde{u}, 0, 0)$ . Since the elements

$$\frac{\partial v'}{\partial u}, \quad \frac{\partial w'}{\partial u}, \quad \frac{\partial w'}{\partial v}, \quad \text{and} \quad \frac{\partial w'}{\partial w}$$

are all 0 at equilibrium, then the eigenvalues of the Jacobian matrix are

$$\frac{\partial u'}{\partial u}, \quad \frac{\partial v'}{\partial v} \quad \text{and} \quad 0.$$

The equilibrium point  $(\tilde{u}, 0, 0)$  is locally stable if each of these eigenvalues are lower than one in absolute value. But since  $\tilde{u}$  is a fixed point of the recurrence system (1), then we must have, at equilibrium,

$$\left| \frac{\partial u'}{\partial u} \right| < 1 .$$

Thus, we just need to analyse the eigenvalue  $\partial v'/\partial v$  at equilibrium, which is

$$\frac{\partial v'}{\partial v} \Big|_{(\tilde{u}, 0, 0)} = \tilde{u} \frac{\partial}{\partial v} \tilde{P}_{uv} + \tilde{P}_{vv} + (1 - \tilde{u}) \frac{\partial}{\partial v} \tilde{P}_{rv} ,$$

where  $\tilde{P}_{ij}$  is the value of  $P_{ij}$  at equilibrium. But we have

$$\begin{aligned} \frac{\partial}{\partial v} \tilde{P}_{uv} &= \frac{(1 - \tilde{P}_{ur})}{2\tilde{u}} \left[ \frac{\mu(1 - \alpha_{11}) + \mu\beta(\alpha_{11} + \alpha_{12})\tilde{u}}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] , \\ \tilde{P}_{vv} &= (1 - \tilde{P}_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{12}) + \mu\beta\alpha_{11}\tilde{u}} \right] , \\ \frac{\partial}{\partial v} \tilde{P}_{rv} &= \frac{(1 - \tilde{P}_{rr})}{2\tilde{u}} \left( \frac{\alpha_{11} + \alpha_{12}}{\alpha_{11}} \right) \\ &= \frac{\tilde{P}_{ur}}{2(1 - \tilde{u})} \left( \frac{\alpha_{11} + \alpha_{12}}{\alpha_{11}} \right) , \end{aligned}$$

the last equality coming from a relation existing at equilibrium, that is

$$\begin{aligned} \tilde{u} &= \tilde{u}\tilde{P}_{uu} + (1 - \tilde{u})\tilde{P}_{ru} \\ &= \tilde{u}(1 - \tilde{P}_{ur}) + (1 - \tilde{u})(1 - \tilde{P}_{rr}) . \end{aligned} \tag{B1}$$

The transition probabilities  $\tilde{P}_{ur}$  and  $\tilde{P}_{vr}$  are

$$\begin{aligned} \tilde{P}_{ur} &= \exp \{ -[\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}] \} , \\ \tilde{P}_{vr} &= \exp \{ -[\mu(1 - \alpha_{12}) + \mu\beta\alpha_{11}\tilde{u}] \} . \end{aligned}$$

Finally, we get

$$\begin{aligned} \frac{\partial v'}{\partial v} \Big|_{(\tilde{u}, 0, 0)} &= \frac{1}{2} \left\{ 1 + (1 - \tilde{P}_{vr}) \frac{\mu(1 - \alpha_{12})}{\mu(1 - \alpha_{12}) + \mu\beta\alpha_{11}\tilde{u}} \right. \\ &\quad \left. + \frac{\alpha_{12}}{\alpha_{11}} \left[ 1 - (1 - \tilde{P}_{ur}) \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \right\} . \end{aligned}$$

This quantity, which is positive, is strictly less than 1 if and only if

$$\begin{aligned} &\frac{1}{\alpha_{11}} \left[ 1 - \{ 1 - e^{-[\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]} \} \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &< \frac{1}{\alpha_{12}} \left[ 1 - \{ 1 - e^{-[\mu(1 - \alpha_{12}) + \mu\beta\alpha_{11}\tilde{u}]} \} \frac{\mu(1 - \alpha_{12})}{\mu(1 - \alpha_{12}) + \mu\beta\alpha_{11}\tilde{u}} \right] . \quad \square \end{aligned}$$

To derive the result obtained by Motro (1982b), we let  $\mu$  go to infinity. In that case, the equilibrium point  $\tilde{u}$  of (1) approaches 1, so that the expression

$$\frac{1}{\alpha} \left[ 1 - \{1 - e^{-[\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}]}\} \frac{\mu(1-\alpha)}{\mu(1-\alpha) + \mu\beta\alpha_{11}\tilde{u}} \right]$$

approaches

$$A(\alpha_{11}, \alpha) = \frac{1}{\alpha} \left[ 1 - \frac{1-\alpha}{1-\alpha + \beta\alpha_{11}} \right].$$

We have to find a value  $\alpha_{11}$  for which

$$A(\alpha_{11}, \alpha_{11}) < A(\alpha_{11}, \alpha) \quad \text{for all } \alpha \neq \alpha_{11}.$$

We have

$$\left. \frac{\partial}{\partial \alpha} A(\alpha_{11}, \alpha) \right|_{\alpha=\alpha_{11}} = \frac{-\beta\alpha_{11}(1 - 2\alpha_{11} + \beta\alpha_{11})}{\alpha_{11}^2(1 - \alpha_{11} + \beta\alpha_{11})^2},$$

which is 0 when

$$\alpha_{11} = \frac{1}{2 - \beta}.$$

Moreover, the second order partial derivative

$$\left. \frac{\partial^2}{\partial \alpha^2} A(\alpha_{11}, \alpha) \right|_{\alpha=\alpha_{11}} = \frac{2\beta\alpha_{11}}{\alpha_{11}(1 - \alpha_{11} + \beta\alpha_{11})^2} + \frac{2\beta\alpha_{11}(1 - 2\alpha_{11} + \beta\alpha_{11})^2}{\alpha_{11}^3(1 - \alpha_{11} + \beta\alpha_{11})^3}$$

is positive at  $\alpha_{11} = 1/(2 - \beta)$ . Thus we have convergence of the optimal migration rate to the value  $1/(2 - \beta)$ .

### B.2 Proof of Result 5.3

As in the previous section, we only have to analyse the eigenvalue

$$\left. \frac{\partial v'}{\partial v} \right|_{(\tilde{u}, 0, 0)} = \tilde{u} \frac{\partial}{\partial v} \tilde{P}_{uv} + \tilde{P}_{vv} + (1 - \tilde{u}) \frac{\partial}{\partial v} \tilde{P}_{rv},$$

where

$$\frac{\partial}{\partial v} \tilde{P}_{uv} = \frac{(1 - \tilde{P}_{ur})}{\tilde{u}} \left[ \frac{\mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{12}\tilde{u}}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right],$$

$$\tilde{P}_{vv} = (1 - \tilde{P}_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{11}\tilde{u}} \right],$$

$$\frac{\partial}{\partial v} \tilde{P}_{rv} = \frac{(1 - \tilde{P}_{rr})}{\tilde{u}} \begin{pmatrix} \alpha_{12} \\ \alpha_{11} \end{pmatrix}$$

$$= \frac{\tilde{P}_{ur}}{1 - \tilde{u}} \begin{pmatrix} \alpha_{12} \\ \alpha_{11} \end{pmatrix}.$$

The quantities  $\tilde{P}_{ur}$  and  $\tilde{P}_{vr}$  are

$$\begin{aligned} \tilde{P}_{ur} &= \exp \{ -[\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}] \}, \\ \tilde{P}_{vr} &= \exp \{ -[\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{11}\tilde{u}] \}. \end{aligned}$$

Thus, we have

$$\begin{aligned} \left. \frac{\partial v'}{\partial v} \right|_{(\tilde{u}, 0, 0)} &= (1 - \tilde{P}_{ur}) \left[ \frac{\mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{12}\tilde{u}}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + (1 - \tilde{P}_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + \tilde{P}_{ur} \left( \frac{\alpha_{12}}{\alpha_{11}} \right) \\ &= (1 - \tilde{P}_{ur}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + (1 - \tilde{P}_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + \frac{\alpha_{12}}{\alpha_{11}} \left[ 1 - (1 - \tilde{P}_{ur}) \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right]. \end{aligned}$$

This quantity is always positive, and is strictly less than 1 if and only if

$$\begin{aligned} &\frac{1}{\alpha_{11}} \left\{ 1 - (1 - \tilde{P}_{ur}) \left[ \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \right\} \\ &< \frac{1}{\alpha_{12}} \left\{ 1 - (1 - \tilde{P}_{ur}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \right. \\ &\quad \left. - (1 - \tilde{P}_{vr}) \left[ \frac{\mu(1 - \alpha_{12})/2}{\mu(1 - \alpha_{11})/2 + \mu(1 - \alpha_{12})/2 + \mu\beta\alpha_{11}\tilde{u}} \right] \right\}. \quad \square \end{aligned}$$

We now derive the result obtained by Motro (1983). The expression

$$\frac{1}{\alpha} [1 - G(\alpha_{11}, \alpha)]$$

given in result (5.3) converges, when  $\mu$  approaches infinity, to the expression

$$B(\alpha_{11}, \alpha) = \frac{1}{\alpha} \left[ 1 - \frac{(1 - \alpha)/2}{1 - \alpha_{11} + \beta\alpha_{11}} - \frac{(1 - \alpha)/2}{(1 - \alpha_{11})/2 + (1 - \alpha)/2 + \beta\alpha_{11}} \right],$$

whose first partial derivative

$$\left. \frac{\partial}{\partial \alpha} B(\alpha_{11}, \alpha) \right|_{\alpha=\alpha_{11}} = \frac{(3 - 4\beta) + \alpha_{11}(3 - 2\beta)(2\beta - 1)}{4\alpha_{11}(1 - \alpha_{11} + \alpha_{11}\beta)^2}$$

is 0 at

$$\alpha_{11} = \frac{4\beta - 3}{(3 - 2\beta)(2\beta - 1)}$$

when  $\beta > \frac{3}{4}$ . At this value for  $\alpha_{11}$ , the second partial derivative simplifies to

$$\left. \frac{\partial^2}{\partial \alpha^2} B(\alpha_{11}, \alpha) \right|_{\alpha = \alpha_{11}} = \frac{(3 - 2\beta)(1 - 2\beta)^4}{2\beta^2(4\beta - 3)},$$

which is positive.

When  $\beta \leq \frac{3}{4}$ , we have

$$\frac{\partial}{\partial \alpha} B(0, \alpha) = \frac{1}{2(2 - \alpha)^2},$$

which is positive for every  $\alpha$ , so that we have

$$\begin{aligned} B(0, \alpha) &= \frac{3 - \alpha}{2(2 - \alpha)} \\ &> \frac{3}{4} \quad \text{for all } \alpha \neq 0, \end{aligned}$$

and

$$\begin{aligned} \lim_{\alpha_{11} \rightarrow 0} B(\alpha_{11}, \alpha_{11}) &= \lim_{\alpha_{11} \rightarrow 0} \frac{1}{\alpha_{11}} \left[ 1 - \frac{1 - \alpha_{11}}{1 - \alpha_{11} + \beta \alpha_{11}} \right] \\ &= \beta \\ &\leq \frac{3}{4}. \end{aligned}$$

Therefore  $B(\alpha_{11}, \alpha_{11}) < B(\alpha_{11}, \alpha)$  for all  $\alpha \neq \alpha_{11}$ , where

$$\alpha_{11} = \begin{cases} 0 & \text{if } 0 < \beta \leq \frac{3}{4} \\ \frac{\beta - \frac{3}{4}}{(\beta - \frac{1}{2})(\frac{3}{2} - \beta)} & \text{if } \frac{3}{4} < \beta \leq 1 \end{cases}.$$

### Appendix C

#### C.1 A criterion for local stability with an eigenvalue 1

In this section we only recall a result presented in Morris, Matessi and Karlin (1987), generalizing a result of Lessard and Karlin (1982).

Let  $T(\mathbf{x}) = (T_1(\mathbf{x}), \dots, T_n(\mathbf{x}))$  be a transformation of a frequency vector  $\mathbf{x}$ , which admits an equilibrium point  $\tilde{\mathbf{x}}$ . Suppose that the spectral radius of the Jacobian matrix of  $T$  at equilibrium is 1, and that this matrix is in the general form

$$L = \begin{pmatrix} A & B \\ 0 & C \end{pmatrix},$$

where  $A$  is of order  $m$ ,  $C$  is of order  $n - m$ , and  $A$  and  $B$  are in the form

$$A = \begin{pmatrix} X & 0 \\ Y & Z \end{pmatrix}, \quad B = \begin{pmatrix} V \\ W \end{pmatrix},$$

and where  $X$ ,  $V$  and  $C$  are nonnegative matrices. Moreover, suppose that  $X$  is a primitive matrix of order  $l$ , in the sense that some power of  $X$  is a positive matrix, whose spectral radius is 1, that is  $\rho(X) = 1$ , and that  $Z$  satisfies  $\rho(Z) < 1$ . Let  $\xi$  and  $\eta$  be left and right eigenvectors for  $A$  associated with the eigenvalue 1, chosen such that their scalar product is 1. The first  $l$  components of  $\xi$  give a left eigenvector for  $X$  associated with the eigenvalue 1, while the other components are 0. Also, the first  $l$  components of  $\eta$  give a right eigenvector for  $X$  associated with the eigenvalue 1. These eigenvectors for  $X$  can be chosen positive (all their components are positive) by the Perron-Frobenius theory for nonnegative matrices.

Define the vectors

$$\theta^{(1)} = (\theta_1, \dots, \theta_m), \quad \theta^{(2)} = (\theta_{m+1}, \dots, \theta_n),$$

where

$$\theta_i = \sum_{k=1}^m \sum_{l=1}^m \frac{\partial^2 T_i(\tilde{x})}{\partial x_k \partial x_l} \eta_k \eta_l.$$

We use the notation  $\langle\langle \cdot, \cdot \rangle\rangle$  for the usual scalar product.

**Result C.1** (Lessard and Karlin, 1982; Morris, Matessi and Karlin, 1987). *When*

$$S \stackrel{\text{def}}{=} \langle\langle \xi, \theta^{(1)} + B(I - C)^{-1} \theta^{(2)} \rangle\rangle < 0,$$

*then the equilibrium  $\tilde{x}$  is locally stable. It is unstable when  $S > 0$ .*

### C.2 Proof of Result 4.2

In order to have the Jacobian matrix in the form described above, we consider the linear approximation of the system  $(v', u', w')$  around the equilibrium point  $(0, \tilde{u}, 0)$ :

$$\begin{pmatrix} v' \\ u' - \tilde{u} \\ w' \end{pmatrix} \doteq \begin{pmatrix} 1 & 0 & \frac{\partial v'}{\partial w} \\ \frac{\partial u'}{\partial v} & \frac{\partial u'}{\partial u} & \frac{\partial u'}{\partial w} \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} v \\ u - \tilde{u} \\ w \end{pmatrix},$$

where the derivatives are evaluated at the equilibrium point. Then the matrices  $A$  and  $B$  are

$$A = \left( \begin{array}{cc} 1 & 0 \\ \frac{\partial u'}{\partial v} & \frac{\partial u'}{\partial u} \end{array} \right) \Bigg|_{(0, \tilde{u}, 0)}, \quad B = \left( \begin{array}{c} \frac{\partial v'}{\partial w} \\ \frac{\partial u'}{\partial w} \end{array} \right) \Bigg|_{(0, \tilde{u}, 0)},$$

and the matrix  $C$  is the scalar 0. In order to apply result C.1, it is necessary to verify that the value of  $\partial v'/\partial w$  is nonnegative at equilibrium. Using relation (B1), we get

$$\begin{aligned} \frac{\partial v'}{\partial w} \Bigg|_{(0, \tilde{u}, 0)} &= 1 + (1 - \tilde{P}_{wr}) \left[ \frac{\mu(1 - \alpha_{22})}{\mu(1 - \alpha_{22}) + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + \frac{\alpha_{22}}{\alpha_{11}} \left[ (1 - \tilde{P}_{wr}) \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right], \end{aligned}$$

which is nonnegative. Observe that

$$\frac{\partial u'}{\partial v} \Bigg|_{(0, \tilde{u}, 0)} = -\tilde{P}_{ru} + \tilde{P}_{ur}(\mu\beta\alpha_{11}\tilde{u} - 1) + \tilde{P}_{rr}\mu\beta\alpha_{11}(1 - \tilde{u}),$$

using again relation (B1), and that

$$\begin{aligned} \frac{\partial u'}{\partial u} \Bigg|_{(0, \tilde{u}, 0)} &= 1 - \tilde{P}_{ru} + \tilde{P}_{ur}(\mu\beta\alpha_{11}\tilde{u} - 1) + \tilde{P}_{rr}\mu\beta\alpha_{11}(1 - \tilde{u}) \\ &= 1 + \frac{\partial u'}{\partial v} \Bigg|_{(0, \tilde{u}, 0)}. \end{aligned}$$

Therefore  $\xi = (1, 0)$  and  $\eta = (1, -1)$  are the left and right eigenvectors, respectively, associated with the eigenvalue 1 of  $A$ , whose scalar product is 1. The second component of  $\xi$  being 0, we need only to calculate

$$\begin{aligned} \theta_1 &= \left( \frac{\partial^2 v'}{\partial v^2} - 2 \frac{\partial^2 v'}{\partial u \partial v} + \frac{\partial^2 v'}{\partial u^2} \right) \Bigg|_{(0, \tilde{u}, 0)}, \\ \theta_3 &= \left( \frac{\partial^2 w'}{\partial v^2} - 2 \frac{\partial^2 w'}{\partial u \partial v} + \frac{\partial^2 w'}{\partial u^2} \right) \Bigg|_{(0, \tilde{u}, 0)}. \end{aligned}$$

Using relation (B1) in the expressions for the derivatives, we get

$$\theta_1 = -\frac{1}{\tilde{u}}, \quad \theta_3 = \frac{1}{2\tilde{u}}.$$

Owing to result C.1, we conclude that in the case where

$$S = \frac{1}{2\tilde{u}} \frac{\partial v'}{\partial w} \Bigg|_{(0, \tilde{u}, 0)} - \frac{1}{\tilde{u}} < 0,$$



the equilibrium is locally stable. The expression for  $\partial v'/\partial w$  evaluated at  $(0, \tilde{u}, 0)$  leads to the final result.

C.3 Proof of Result 5.4

As previously, we calculate

$$\begin{aligned} \frac{\partial v'}{\partial w} \Big|_{(0, \tilde{u}, 0)} &= 2 \left[ (1 - \tilde{P}_{rr}) \frac{(1 - \tilde{u})}{\tilde{u}} + 1 - \tilde{P}_{ur} \right] \\ &= 2, \end{aligned}$$

and we show that

$$\left( \frac{\partial u'}{\partial v} - \frac{\partial u'}{\partial u} \right) \Big|_{(0, \tilde{u}, 0)} = -1.$$

Then  $\xi = (1, 0)$  and  $\eta = (1, -1)$  are the left and right eigenvectors associated with the eigenvalue 1 of the matrix  $A$ , whose scalar product is 1, and we need only to calculate

$$\begin{aligned} \theta_1 &= \left( \frac{\partial^2 v'}{\partial v^2} - 2 \frac{\partial^2 v'}{\partial u \partial v} + \frac{\partial^2 v'}{\partial u^2} \right) \Big|_{(0, \tilde{u}, 0)}, \\ \theta_3 &= \left( \frac{\partial^2 w'}{\partial v^2} - 2 \frac{\partial^2 w'}{\partial u \partial v} + \frac{\partial^2 w'}{\partial u^2} \right) \Big|_{(0, \tilde{u}, 0)}. \end{aligned}$$

We get

$$\begin{aligned} \theta_1 &= -\frac{1}{\tilde{u}} \left\{ 1 - (1 - \tilde{P}_{ur}) \left[ \frac{\mu(1 - \alpha_{11})/2}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right]^2 \right. \\ &\quad + \tilde{P}_{ur} \left[ \frac{[\mu(1 - \alpha_{11})/2]^2}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \\ &\quad + (1 - \tilde{P}_{ur}) \left[ \frac{\mu^2(1 - \alpha_{11})(1 - \alpha)/4}{[\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}]^2} \right] \\ &\quad \left. - \tilde{P}_{ur} \left[ \frac{\mu^2(1 - \alpha_{11})(1 - \alpha)/4}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \right\}, \\ \theta_3 &= \frac{1}{2\tilde{u}} \left\{ \frac{\alpha_{22}}{\alpha_{11}} \left[ 1 - (1 - \tilde{P}_{ur}) \frac{\mu(1 - \alpha_{11})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right] \right. \\ &\quad \left. + (1 - \tilde{P}_{ur}) \frac{\mu(1 - \alpha_{22})}{\mu(1 - \alpha_{11}) + \mu\beta\alpha_{11}\tilde{u}} \right\}. \end{aligned}$$

Therefore, owing to result C.1, the equilibrium is locally stable when

$$S = \theta_1 + 2\theta_3 < 0.$$

The above expressions for  $\theta_1$  and  $\theta_3$  yield the final result.

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