

# An inclusive fitness model for the sex ratio in a partially sibmating population with inbreeding cost

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## Summary

We construct an inclusive fitness model to find the evolutionarily stable sex ratios in a partially sibmating diploid or haplodiploid population. We assume a constant rate of sibmating with inbred offspring incurring a fitness penalty which, under haplodiploidy, is only suffered by females. We construct a one-locus genetic model for the same problem and observe that when selection is weak it gives the same numerical results as the inclusive fitness model.

*Keywords:* sex ratio; sibmating; inbreeding depression; haplodiploid; inclusive fitness; one-locus genetic model

## Introduction

Fisher (1930) argued that in a randomly mating sexual population, evolutionary forces should produce a 1:1 sex ratio. Hamilton (1967) was the first to point out that certain asymmetries between the sexes of a genetic or behavioural nature can invalidate Fisher's argument and create a bias in what he termed the 'unbeatable' sex ratio. Our purpose is to investigate the effect on the sex ratio of such asymmetries in a partially sibmating population in which inbred offspring suffer a viability cost, and to compare our results for diploid and haplodiploid genetic systems. Much previous work has focused on different aspects of this investigation, and we provide a sex-ratio formula which generalizes a number of existing formulae and partitions the sex ratio bias into the three contributing factors of local mate competition, inbreeding, and inbreeding depression.

### *Local mate competition*

Hamilton (1967) modelled local mate competition with a patch structure, in which  $N$  unrelated females breed together on a single patch, and their offspring mate at random on the patch before dispersing into the population at large. In this model, competition between related males (in this case, sibs) for a limited number of matings produces a female-biased sex ratio. An equivalent modelling assumption (Maynard Smith, 1978) is simply to specify that a fixed proportion of all females sibmate, and the rest mate panmictically, and this is the approach we adopt here. Subsequent generalizations of Hamilton's patch-structured model (Frank, 1985; Bulmer, 1986; Taylor, 1988) postulate only partial dispersal by mated females and this introduces a measure of local competition between females for breeding space, which can reduce the bias in the sex ratio, depending as it does on the extent of the asymmetry in local resource competition between males

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and females (Taylor, 1981). The effects of inbreeding depression are more difficult to analyze when dispersal is partial.

### *Inbreeding*

When relatives compete with one another for reproductive resources (in particular for mates) there is a tendency for mating to take place between relatives, and this natural association between inbreeding and LMC has often caused them to be confounded in the sex-ratio literature. The question arises as to how much of the bias is due to each of the factors of local mate competition and inbreeding and Herre (1985) was the first to attempt to partition these two effects for a haplodiploid population; our formula is a generalization of his. It is possible to construct examples in which there is LMC but no inbreeding and vice versa, but such models are often contrived.

### *Haplodiploidy*

Haplodiploid populations are typically arrhenotokous, such that haploid males and diploid females develop from unfertilized and fertilized eggs respectively. The resulting genetic asymmetry between the sexes has an important effect on the sex ratio. Most importantly, it creates a different relatedness of a mother to her sons and to her daughters, these being 1 and  $\frac{1}{2}$  respectively in an outbreeding population. In the absence of complicating factors such as inbreeding and LMC this asymmetry does not produce a sex ratio bias since the reproductive value of a male is half that of a female (Price, 1970). However, an effect of inbreeding is that the relatedness of a mother to her daughter increases, while that to her son remains the same, and this produces a female bias in the ESS sex ratio. This effect of inbreeding *per se* is not found in diploid populations in which there is no relatedness asymmetry.

### *Cost of inbreeding*

Inbreeding depression, caused by the expression of deleterious recessive alleles in the homozygous state, generally tends to reduce fitness (Falconer, 1989). For example, Miller *et al.* (1993) found that inbred males in *Drosophila melanogaster* had a significant reduction in mating ability and therefore in reproductive fitness, and Taylor and Getz (1994) constructed a model to show that inbreeding depression reduced the selective advantages of sibmating. But is inbreeding depression by itself expected to bias the sex ratio? In diploid populations the answer is expected to be no, as inbreeding depression affects males and females equally. However, in the presence of local mate competition, inbreeding depression causes a slight reduction in the female bias; this effect was first studied by Charlesworth and Charlesworth (1981) in a population of self-fertile hermaphrodites. In haplodiploid populations, only the female suffers the cost of inbreeding and this provides a new component to the asymmetry between the sexes and alters the effect described above.

Our models assume an infinite population with non-overlapping generations. We assume that females mate once, with a sib with probability  $p$  and panmictically with probability  $1 - p$ . Offspring of sibmated parents (both sexes under diploidy, only females under haplodiploidy) survive to breed with probability  $1 - s$  relative to outbred offspring. These assumptions follow the model of Kaitala and Getz (1992) except we have no male-mating cost  $\mu$  and we impose an inbreeding cost.

We have two objectives. The first is to formulate an inclusive fitness sex-ratio model for the given population structure for both diploidy and haplodiploidy, and display the effects of the

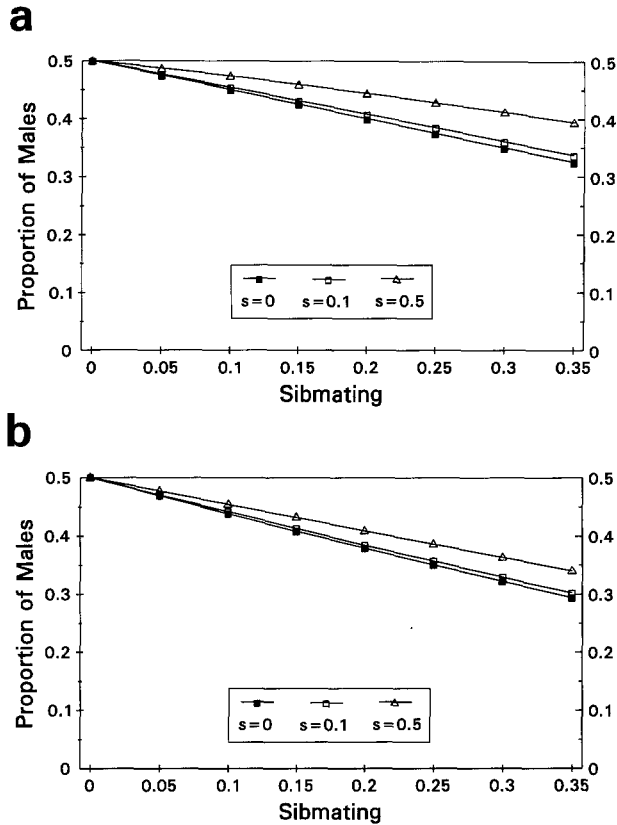


Figure 1. These graphs show the effect of sibmating on the sex ratio for different values of inbreeding depression  $s$  under (a) diploidy and (b) haplodiploidy. The inclusive fitness model with  $s = 0$  is the same as the LMC models of Hamilton (1979) and Taylor and Bulmer (1980), with  $p = 1/N$ . Increased inbreeding depression slightly reduces the female bias under both genetic systems. This effect is greater under diploidy than under haplodiploidy.

various factors described above. The second is to check this argument with a one-locus genetics model for the special case of a rare dominant mutant.

## Results

The inclusive fitness model provides the following formula for the sex ratio  $\alpha$  (proportion of males):

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{2r_m v_m}{r_f v_f + r_m v_m} \right] \cdot \left[ \frac{V_o}{(1 - p)V_o + pV_s} \right] \quad (1)$$

where  $p$  is the probability a female will sibmate,  $r_i$  is the relatedness of a mother to her sex  $i$  offspring,  $v_i$  is the reproductive value of sex  $i$ , and  $V_o$  and  $V_s$  are the reproductive values of a single outbreeding and sibmating respectively. The model is presented in Appendix A, and the formula is displayed graphically in Fig. 1. The terms in the square brackets in Equation (1) can be associated with the three principle factors affecting the sex ratio. The first is the local mate

competition term, the second provides the effect of inbreeding, and the third gives the effect of inbreeding depression.

In Appendix A, we show that under diploidy, the inbreeding term is unity, and Equation (1) becomes

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{1}{1 - ps} \right] \quad (2)$$

first obtained by Charlesworth and Charlesworth (1981) in a population of self-fertile hermaphrodites. Here,  $p$  is their rate of selfing  $S$ , and  $s$  is their fitness penalty  $\delta$  paid by selfed seeds. Under haplodiploidy, Equation (1) becomes

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{4 - 2p}{4 - p} \right] \cdot \left[ \frac{3}{3 - 2ps - p^2s} \right] \quad (3)$$

and in case there is no inbreeding penalty,  $s = 0$  and the last term is unity, giving

$$\alpha = \frac{1}{2} \cdot [1 - p] \cdot \left[ \frac{4 - 2p}{4 - p} \right] \quad (4)$$

which is Herre's (1985) formula.

For the associated one-locus genetic model, with a rare dominant mutant, the equations of mating type frequencies are presented in Appendix B. ESS sex ratios were calculated by numerical solution of the equations and were found to be identical to those provided by the inclusive fitness Equation (1).

## Discussion

The three terms in the square brackets in Equation (1) can be associated with the three principle factors affecting the sex ratio. The effect of the local mate competition term  $1 - p$  is greater for higher inbreeding probability  $p$ ; indeed, a mother receives an inclusive fitness gain through an extra son only when he outbreeds, and so the benefit of this extra male is less when the population-wide level of sibmating is high.

The second term measures the effect of inbreeding. The product of relatedness  $r$  and reproductive value  $v$  might be called the 'complete relatedness' and this inbreeding term introduces a bias when the complete relatedness of a mother to her sons is different from that to her daughters. The genetic symmetry of diploidy guarantees that the two complete relatedness coefficients are always the same, regardless of the amount of inbreeding. Under haplodiploidy, in the absence of inbreeding, the complete relatednesses are also the same, but an effect of inbreeding is to increase the relatedness of a mother to her daughter, while that to her son remains the same, and this increases the female bias in the ESS sex ratio.

The third term measures the effect of an inbreeding cost, and this modifies the sex-ratio bias whenever a sibmating and an outbred mating have different reproductive values. Under both genetic systems, when there is an inbreeding penalty, a sibmating will always be less valuable than an outbreeding because inbred offspring survive to breed with a lower probability. Thus  $V_s < V_o$  and the last term in Equation (1) will always reduce the female bias.

It is at first surprising that there is an effect of the inbreeding under diploidy, since, in this case, the two sexes incur the viability penalty equally. In fact, the effect works, not through any genetic asymmetry, but by modifying the behavioural asymmetry already caused by the LMC. Indeed, recall that the inclusive fitness gain to a mother through an extra son accrues only through his

outbreedings, and this is unaffected by an inbreeding cost. However, the mother does receive a fitness gain through an extra daughter who sibmates (as well as through one who outbreeds), and this gain is reduced by the inbreeding penalty. So the inbreeding penalty reduces the marginal gain through daughters, but does not affect that through sons, and therefore reduces the existing female-bias. This effect was first studied by Charlesworth and Charlesworth (1981) in a diploid population.

In fact, it is interesting to note that this effect of inbreeding depression is greater under diploidy than under haplodiploidy, that is, the last term in Equation (2) is greater than the last term in Equation (3). We can attribute this to the genetic asymmetry of haplodiploidy. The value of a sibmating is greater under haplodiploidy than under diploidy because haploid males do not pay an inbreeding cost, and thus, the reduction in the inclusive fitness gain through daughters, caused by the inbreeding penalty, is of less magnitude.

In a haplodiploid population with no inbreeding cost ( $s = 0$ ), the ESS sex ratio (Equation 4) was first obtained by Hamilton (1979), and Taylor and Bulmer (1980) working with an equivalent patch-structured model with  $N$  females per patch and  $p = 1/N$ . It was Herre (1985) who first partitioned this formula into an LMC and an inbreeding component. Herre's approach was to let the number  $n$  of females per patch be variable in the population, and to allow the female to respond to variations in  $n$ , but not, of course, to her own inbreeding coefficient, and this allowed him to separate out the common factor due to inbreeding. The value of  $p$  used in his formula is  $1/N$  where  $N$  is the harmonic mean of  $n$ .

In Appendix A (Equation A3) we verify the convergence stability (Christiansen, 1991) of the sex ratio. This condition is the essential ingredient of what Eshel (1983) called continuous stability (CSS), and what Taylor (1989) subsequently referred to as  $m$ -stability. A discussion of the various stability conditions that have been identified can get quite technical; we will only point out that the inclusive fitness arguments in general are able to check the convergence stability of an equilibrium.

Kaitala and Getz (1992) use a one-locus genetic model similar to that laid out in Appendix B to study the sex ratio in a partially sibmating haplodiploid population with no inbreeding penalty and a male mating cost  $\mu$ . Their numerical results, for the case  $\mu = 0$ , are slightly different from the predictions of Equation (4), and they account for the discrepancy between their results and those of Taylor and Bulmer (1980) by suggesting that a perturbation to the sibmating frequency occurs when a mutant female arrives on a patch. But in a weak-selection model, this perturbation is negligible and the difference between the results is now understood to be due to a normalization error in their equations.

The calculations of the one-locus genetic model in Appendix B make the assumption of a rare mutant and this makes the recursion equations for the  $8 \times 8$  matrix much simpler. We have found that this assumption has a negligible effect; the one-locus genetic model in Appendix B which assumes a rare mutant gives the same numerical results as the corrected genetic model of Kaitala and Getz (1992) which does not assume a rare mutant. Our genetic model also employs a dominant mutant. Several authors, including Bulmer (1986) and Kaitala and Getz (1992), have shown that dominance has negligible effects when selection is weak; inclusive fitness and one-locus genetic models continue to give the same results.

Under the assumptions of weak selection and additive gene action our inclusive fitness analysis provides the same numerical results as the one-locus genetic model described in Appendix B. This illustrates a general equivalence between these two modelling approaches which has been discussed by several authors including Hamilton (1975), Charlesworth (1980), Grafen (1985), Bulmer (1986) and Taylor (1989). The inclusive fitness approach is important because the formula it provides allows us to understand how different factors contribute to the sex-ratio bias,

and in particular to pin down the crucial role played by reproductive value in evolutionary modelling.

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### Appendix A: the inclusive fitness model

First we define the necessary notation:

- $\alpha$  the sex ratio (proportion of males), assumed uniform in the population
- $p$  the probability of sibmating
- $F$  the average inbreeding coefficient among breeding females
- $s_m$  the viability penalty suffered by male offspring of a sibmating
- $s_f$  the viability penalty suffered by female offspring of a sibmating
- $r_i$  the relatedness of a mother to her sex  $i$  ( $i = m$  or  $f$ ) offspring
- $v_i$  the reproductive value of sex  $i$  ( $i = m$  or  $f$ )
- $V_s$  the reproductive value of a single sibmating
- $V_o$  the reproductive value of a single outbreeding

The inclusive fitness gain to a mother through an extra male offspring is

$$W_m = (1 - ps_m) \frac{1 - \alpha}{\alpha} \frac{(1 - ps_f)}{(1 - ps_m)} (1 - p) V_o r_m V_m \quad (\text{A1})$$

The terms are explained as follows. The average male survives with probability  $p(1 - s_m) + (1 - p) = (1 - ps_m)$  and increases his mother's fitness only when he outbreeds since a sibmating will take away a mating opportunity from another son. The expected number of matings per male is the breeding sex ratio which is  $[(1 - \alpha)(1 - ps_f)]/[\alpha(1 - ps_m)]$  where the average female survives with probability  $(1 - ps_f)$ . A proportion  $(1 - p)$  of these matings are outbreedings. Note that the male gains proportion  $v_m$  of the value  $V_o$  of each outbreeding. The inclusive fitness gain through an extra female offspring is

$$W_f = (1 - ps_f)[(1 - p)V_o r_f v_f + pV_s(r_f v_f + r_m v_m)] \quad (\text{A2})$$

where an extra female offspring survives with probability  $(1 - ps_f)$  and increases her mother's inclusive fitness whether she outbreeds (first term in square brackets) or sibmates (second term in square brackets). In the case where she sibmates, she also gives a sibmating to her brother and this accounts for the sum of the two  $r_i v_i$  terms. At equilibrium,  $W_m = W_f$ , and we obtain the ESS sex ratio, Equation (1). The derivative

$$\frac{d}{d\alpha} [w_m(\alpha) - w_f(\alpha)] = - \frac{(1 - ps_f)(1 - p)V_o r_m v_m}{\alpha^2} \quad (\text{A3})$$

is negative, therefore the sex ratio is convergence stable (Christiansen 1991).

To calculate the ESS sex ratios in Equation (1) we need to find relatedness and reproductive values under both genetic systems. The general equations for the relative reproductive values of a sibmating and an outbreeding are

$$\begin{aligned} V_s &= (1 - ps_f)(1 - ps_m) - (1 - p)[(1 - ps_f)v_m s_m + (1 - ps_m)v_f s_f] \\ V_o &= 1 - ps_m \end{aligned} \quad (\text{A4})$$

These are calculated from recursion equations, an example of which is given below for the specific case of haplodiploidy.

*Diploidy*

Under diploidy, we have (Michod and Hamilton 1980; Price 1970):

$$r_m = r_f = \frac{1 + 3F}{2(1 + 2F)} \quad v_m = v_f = \frac{1}{2} \quad (\text{A5})$$

Using Equations (A4) and (A5) with  $s_m = s_f = s$ , the relative values of an outbreeding and a sibmating are

$$\begin{aligned} V_s &= (1 - s) \\ V_o &= 1 \end{aligned} \quad (\text{A6})$$

and, using Equations (A5), (A6) and (1), the ESS sex ratio in the diploid case is given by Equation (2).

*Haplodiploidy*

The inbreeding coefficient  $F$  for haplodiploidy is calculated from the following one-generation recursion (Taylor 1993)

$$F = p \left[ \frac{1}{2} \frac{1 + F}{2} + \frac{1}{2} F \right] \quad (\text{A7})$$

where  $F$  on the left is the probability that random alleles from a mated pair are identical by descent. This will happen only when the pair is sibmated which occurs with probability  $p$ . In this case, the probability of identity when the female allele is maternal (*probability* = 1/2) or paternal (*probability* = 1/2) is given by the first and second terms in the brackets respectively. Solving for  $F$  in Equation (A7) gives

$$f = \frac{p}{4 - 3p} \quad (\text{A8})$$

It follows from Equation (A8) that the relatedness coefficients are (Hamilton, 1972; Michod and Hamilton, 1980):

$$r_m = 1, \quad r_f = \frac{1 + 3F}{2 + 2F} = \frac{1}{2 - p} \quad (\text{A9})$$

Following the method of Taylor and Getz (1994), we show that the relative reproductive values of the two types of matings are:

$$\text{sibmating} \quad V_s = 1 - \frac{2s}{3} - \frac{ps}{3} \quad (\text{A10})$$

$$\text{outbreeding} \quad V_o = 1 \quad (\text{A11})$$

We first calculate the number of offspring from each mating type that survive to maturity. The number of male offspring from a mating of either type is

$$m = K\alpha \quad (\text{A12})$$

where  $K$  is the total number of offspring from a mating and the number of breeding daughters is:

$$\text{sibmating} \quad f_s = K[(1 - \alpha)(1 - s)] \quad (\text{A13})$$

$$\text{outbreeding} \quad f_o = K(1 - \alpha) \quad (\text{A14})$$



We normalize these values according to the assumption that the average number of breeding daughters from a mating is unity:

$$pf_s + (1 - p)f_o = 1 \quad (\text{A15})$$

which gives us  $K = 1/[1 - \alpha(1 - ps)]$ . The recursions for the reproductive values of a single sibmating and a single outbreeding are

$$\begin{aligned} V'_s &= pf_s V_s + (1 - p)f_s v_f V_o + \frac{m(1 - p)}{m} v_m V_o \\ &= \frac{p(1 - s)}{(1 - ps)} V_s + \frac{(1 - p)}{(1 - ps)} \left(1 - \frac{2s + ps}{3}\right) V_o \end{aligned} \quad (\text{A16})$$

$$\begin{aligned} V'_o &= pf_o V_s + (1 - p)f_o v_f V_o + \frac{(1 - p)m}{m} v_m V_o \\ &= \frac{p}{(1 - ps)} V_s + \frac{(1 - p)}{(1 - ps)} \left(1 - \frac{ps}{3}\right) V_o \end{aligned} \quad (\text{A17})$$

These are obtained by counting the number of matings of each type by the offspring of each mating type. As an example, we provide the argument for Equation (A16). From a sibmating, there are  $pf_s$  offspring that sibmate each giving her brother a mating, so that in this case we get the entire value  $V_s$  of the sibmating. In addition, there are  $(1 - p)f_s$  female offspring that outbreed providing a value of  $v_f V_o$ . From Equations (A12) and (A15) the breeding sex ratio is  $1/m$ , so each of the  $m$  males can expect  $(1 - p)/m$  outbreedings with value  $v_m V_o$ . To get the second line of Equation (A16) we have used the fact that  $v_f = 2/3$  and  $v_m = 1/3$  (Price, 1970). These recursions can be written in matrix form:

$$\begin{pmatrix} V'_s \\ V'_o \end{pmatrix} = \frac{1}{(1 - ps)} \begin{pmatrix} (1 - s)p & (1 - p)\left(1 - \frac{2s + ps}{3}\right) \\ p & (1 - p)\left(1 - \frac{ps}{3}\right) \end{pmatrix} \begin{pmatrix} V_s \\ V_o \end{pmatrix} \quad (\text{A18})$$

The dominant eigenvalue of this linear system is calculated to be unity and the corresponding dominant eigenvector gives the reproductive values at equilibrium:

$$\begin{pmatrix} V_s \\ V_o \end{pmatrix} = \begin{pmatrix} 1 - \frac{2s}{3} - \frac{ps}{3} \\ 1 \end{pmatrix} \quad (\text{A19})$$

The ESS sex ratio in the haplodiploid case (using Equations (A9)–(A11), (A19) and (1)) is given by Equation (3).

### Appendix B: the one-locus genetic model for the haplodiploid case

We assume that females of genotype  $i$  produce a proportion  $\beta_i$  of males. Let  $x_{ij}(t)$  be the frequency of sibmatings between a type  $i$  female and a type  $j$  male in the population at time  $t$ . Similarly, let  $y_{ij}(t)$  be the frequency of outbreedings such that

$$\sum_{ij} [x_{ij}(t) + y_{ij}(t)] = 1 \quad (\text{B1})$$

The following recursion equations are based on the assumption of a rare and dominant mutant allele B and a wild-type allele b, so that outbreedings of the type Bb  $\times$  B and BB  $\times$  B are assumed to be of negligible frequency:  $y_{22}(t) = 0$  and  $y_{32}(t) = 0$ . The mating type BB  $\times$  B is

omitted as we are only concerned with mutant mating types. All frequencies are normalized by the factor  $K = 1/[(1 - \beta_1)(1 - ps)]$ , so that the average number of breeding daughters is unity.

Sibmatings:

$$x_{12}(t + 1) = \frac{K}{4}(1 - \beta_2)[(1 - s)px_{21}(t) + py_{21}(t)] \quad (\text{B2})$$

$$x_{21}(t + 1) = \frac{1}{(1 - ps)}[(1 - s)px_{12}(t) + py_{12}(t) + \frac{K}{4}(1 - \beta_2)[(1 - s)p(x_{21}(t) + x_{22}(t)) + py_{21}(t)]] \quad (\text{B3})$$

$$x_{22}(t + 1) = \frac{K}{4}(1 - \beta_2)[(1 - s)p(x_{21}(t) + x_{22}(t)) + py_{21}(t)] + K(1 - \beta_3)[(1 - s)px_{31}(t) + py_{31}(t)] \quad (\text{B4})$$

$$x_{31}(t + 1) = \frac{K}{4}(1 - \beta_2)(1 - s)px_{22}(t) \quad (\text{B5})$$

$$x_{32}(t + 1) = \frac{K}{4}(1 - \beta_2)(1 - s)px_{22}(t) + K(1 - \beta_3)(1 - s)px_{32}(t) \quad (\text{B6})$$

Outbreedings:

$$y_{12}(t + 1) = \frac{1}{2} \frac{\beta_2}{\beta_1}(1 - p)[x_{21}(t) + x_{22}(t) + y_{21}(t)] + \frac{\beta_3}{\beta_1}(1 - p)[x_{31}(t) + x_{32}(t) + y_{31}(t)] \quad (\text{B7})$$

$$y_{21}(t + 1) = \frac{(1 - p)}{(1 - ps)}[(1 - s)x_{12}(t) + y_{12}(t)] + \frac{K}{2}(1 - \beta_2)(1 - p)[y_{21}(t) + (1 - s)(x_{21}(t) + x_{22}(t))] + K(1 - \beta_3)(1 - p)[(1 - s)x_{31}(t) + y_{31}(t)] \quad (\text{B8})$$

$$y_{31}(t + 1) = \frac{K}{2}(1 - \beta_2)(1 - p)(1 - s)x_{22}(t) + K(1 - \beta_3)(1 - p)(1 - s)x_{32}(t) \quad (\text{B9})$$