

Sex-ratio distortion driven by migration loads

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Abstract

The significance of migration load in driving the evolution of recipient populations has long been documented in population genetics, but its effects have not been linked to the formation of biased sex ratios in natural populations. In this study, we develop a single-locus model to demonstrate how the migration load can shape the primary and secondary sex ratios in dioecious plants where sexual dimorphism is determined by the sex chromosomes (the XX–XY or similar systems). Our results show that migration load can generate an array of sex ratios (from the female- to male-biased primary/secondary sex ratios), depending on the selection systems at the gametophyte and sporophyte stages and on the sex ratio in the migrating seeds. Ovule abortion and the purging of maladaptive genes from the immigrating pollen at the gametophyte stage can alter the primary sex ratio and indirectly alter the secondary sex ratio. The presence of maladaptive sex-linked genes from the migrating pollen and seeds of males facilitates the outcome of the female-biased secondary sex ratios, while the presence of maladaptive sex-linked genes from the migrating seeds of females can lead to the male-biased secondary sex ratios. The detrimental effects of the Y-chromosome from the migrating pollen and seeds can enhance the formation of female-biased primary and secondary sex ratios. These theoretical predictions highlight an alternative approach to the existing sex-ratio theories for interpreting the formation of biased sex ratios in the populations that are subject to the impacts of maladaptive genes from immigrants.

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1. Introduction

Sex ratio can be categorized as the primary and secondary sex ratios. The primary sex ratio refers to the relative frequencies of female to male gametes that are combined to produce zygotes at the gametophyte stage. The secondary sex ratio refers to the ratio of the number of one sex to the number of its opposite sex in a population or the percentage of males or females in a population at the sporophyte stage. Fisher's pioneer work predicted that the secondary sex ratio is expected to approach a unity when parental expenditures on male and female offspring are equal from the inverse frequency-dependent selection (Fisher, 1930). However, the persistence of biased secondary sex ratios in natural populations suggests that the biological mechanisms other than the inverse frequency-dependent selection might exist. Numerical

theories have been proposed to infer the formation of an array of biased secondary sex ratios (Shaw and Mohler, 1953; Hamilton, 1967; Charnov, 1982; Hardy, 2002). In relation to spatially structured populations, a biased secondary sex ratio can be produced by the mechanisms of local mate competition (LMC; Hamilton, 1967), local resource competition (LRC; Clark, 1978), and group selection (Wilson and Colwell, 1981). These existing theories can be classified into the genetic and non-genetic models (e.g., sex allocation theory), and mixture (Geber, 1999). Nevertheless, relationships between the primary/secondary sex ratio and the gene flow among populations adapted to different environments have not been examined (Antolin, 1993).

The reduction in population fitness owing to the maladaptive genes from immigrants is termed as migration load (Wright, 1977, pp. 485–486). The magnitude of migration load is related to the immigration rate and the strength of selection against maladaptive genes (Wright, 1977; Hu and Li, 2003). It is speculated that migration load

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can frequently occur in the natural populations that are subject to the inputs of immigrants from their surrounding populations. Occurrence of the differential mortality of males and females cannot be excluded when maladaptive sex-linked genes from the immigrants exist, resulting in the biased primary/secondary sex ratios. Furthermore, the sex-ratio variation among populations can be brought about when the selection strengths for the maladaptive sex-linked genes from the immigrants change in space, or when the immigration rates of sex-linked genes from a common source change in space. The spatial differential in migration loads between the sexes can lead to biased population sex ratios, which is distinct from the pattern of the spatial segregation of sexes (SSS) within populations (a finer scale) explained with different hypotheses (Bierzychudek and Eckhart, 1988; Eppley, 2001; Nebel, 2005).

The importance of migration load in driving the evolution of a recipient population has long been documented (Wright, 1969, 1977; Barton and Gale, 1993, p. 30) and its significance has been explicitly demonstrated in shaping a species' range (Kirkpatrick and Barton, 1997; Hu and He, 2006). Burt (1995) used an indirect method, i.e. measuring the additive variance of fitness and using Fisher's fundamental theorem of natural selection, to estimate the immigration loads of seeds and pollen dispersal. In *Ipomopsis aggregate*, seeds and pollen from alien populations reduce fitness by the amounts of 0.002 and 0.008 per generation, respectively (Burt, 1995). The order of migration load from seeds or pollen is about 0.08–12% per generation, compared with the mutation load of 0.2–2% per generation in the species examined by Burt (1995). Early theories for plant species did not link the sex ratio to migration loads although the effects of migrating pollen and seeds on altering the sex ratios have been demonstrated (Bulmer and Taylor, 1980; De Jong et al., 2002). Charnov (1982) examined the equilibrium sex ratio in a spatially structured population from the population genetics perspective. However, all these theories are mainly related to Clark's LRC concept (1978), which is difficult to verify in plants because the movement of males and females are distinct from those in the animals. The purpose of this study is to formulate an alternative theory to address the differential sexual mortality owing to the immigration of maladaptive genes.

An earlier study examined several properties of the sexual differential in the migration load under a variety of conditions where males and females were treated as two separate subpopulations connected by mating (Hu, 2006). The analytical relationships between migration load and sex ratio were not derived, but the previous results are applicable to the case of sex-linked modifier genes with indirect effects on the sex ratio (Feldman and Otto, 1989). Here, we continue to study the relationships between migration load and sex ratio in dioecious plants and necessarily extend the earlier theory to the case of sex-linked genes with direct effects on the sex ratio (Hu, 2006). The proposed theory is applicable to the dioecious plants

where sexual dimorphism is determined by the sex chromosomes (the XX–XY or similar systems), such as in *Silene latifolia* (Grant et al., 1994), *Cannabis sativa* L. (Moliterni et al., 2004), and other dioecious plants (Ainsworth, 2000; Moliterni et al., 2004). A dioecious population consists of plants with staminate flowers and pistillate flowers produced on separate plants. The evolution of dioecious plants generated from the cosexuality phases remains dynamic through the processes of sterile mutation or/and resources reallocation in order to avoid inbreeding depression or to achieve a maximum reproductive gain (Sakai and Weller, 1999; Webb, 1999). Although the present study focuses on the simplest but the most studied XX–XY system at the molecular level (Ainsworth, 2000), the same modeling procedure can be applied to other complicate systems to study the relationships between migration load and sex ratio.

Analogous to previous studies (Hu and Li, 2003; Hu and He, 2006; Hu, 2006), selection at the gametophyte and sporophyte stages is taken into account since the expression of some sex-related genes cannot be excluded at each developing phase (Haldane, 1932; Tanksley et al., 1981; Charlesworth and Charlesworth, 1992; Mulcahy et al., 1996). Migration load can be ascribed to either the migrating pollen or the migrating seeds, or both. This can occur at the gametophyte stage when the maladaptive genes from migrating pollen are present, resulting in a biased primary sex ratio. It can also arise at the sporophyte stage when the maladaptive genes from migrating seeds are present, resulting in a biased secondary sex ratio. As demonstrated in Hu (2006), the two stages of migration loads are interrelated because the gametophyte and sporophyte stages are biologically connected in the life cycle of a dioecious plant. Therefore, sexual differential in the migration load at each stage may generate an array of primary and secondary sex ratios (from the male- to female-biased sex ratios).

In the following sections, we first develop a single-locus model that is applicable to the general case under strong or weak selection. The analytical expressions are then derived for the relationships between the migration load and the primary/secondary sex ratio under weak selection at the gametophyte and sporophyte stages. Inferences on the relationships between the migration load and the primary/secondary sex ratio in natural populations are drawn with numerical examples.

2. The model

2.1. Assumptions

Consider a natural population of a dioecious plant species, with constant rates of immigrating pollen and seeds per generation from source populations. This condition may naturally occur in the mainland-island structure of populations where the island populations mainly receive immigrants from the mainland or in a

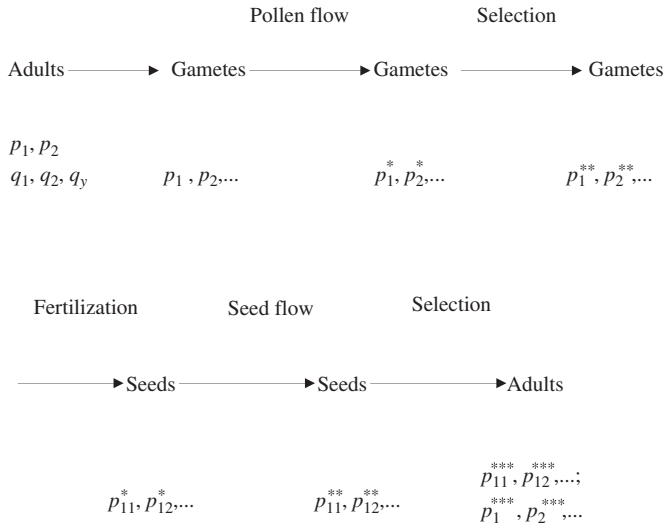


Fig. 1. A scheme shows the life cycle of a dioecious plant. p_1 and p_2 are the frequencies of alleles A and a in the females, respectively. p_{11} and p_{12} are the frequencies of genotypes AA and Aa in the females, respectively. q_1 , q_2 , and q_y are the frequencies of genotypes A , a , and the Y-chromosome in the males, respectively. Different numbers of superscript ‘*’ are used for the variables after different occurrences in the life cycle. Selection is considered after pollen flow at the gametophyte stage and seed flow at the sporophyte stage so that effects of migration load can be examined in the same generation.

continuously distributed species where the marginal populations receive migrants from central populations. The model is distinct from previous models that considered the effects of seed and pollen dispersal distances on the sex ratio (De Jong et al., 2002). Theoretical deduction follows the sequence of events in the plant life cycle: adult generation t , gamete (pollen and ovules) formation, pollen flow, gametophyte selection, mating, seed formation, seed flow, sporophyte selection, and adult generation $t+1$ (Fig. 1).

Mutation rate is assumed to be very small and hence its effect is not included. Population size is assumed to be large so that the effect of genetic drift is negligible. The allele frequencies in ovules before random combinations with pollen or in pollen before the occurrence of immigration are assumed to be the same as those in the preceding adult generation (Wright–Fisher’s model). Only the dioecious plants with the XX–XY system are examined although the same theoretical process can be applied to dioecious plants with the sexual dimorphism being controlled by autosomal genes or other types of sex-linked genes, such as the ZZ–ZW system in *Fragaria elaterea* (Grant, 1999). The effects of Y-chromosome on the fitness are included but its polymorphism on the locus opposite to the locus on the X-chromosome is not considered here.

2.2. General case

Suppose there are N individuals in a dioecious population, with N_{xx} females and N_{xy} males. Let λ_1 be the primary sex ratio generated by the current adults before the

occurrence of migration and natural selection. Let λ_2 be the secondary sex ratio in the current generation and then is set as the ratio N_{xx}/N_{xy} . It can be seen that $\lambda_1 = \lambda_2$ under the assumption of Wright–Fisher’s model. Consider a diallelic sex-linked locus with alleles A_1 and A_2 . In the case of multiple alleles, consider one allele as A_1 and the remaining alleles as A_2 . There are three genotypes A_1A_1 , A_1A_2 , and A_2A_2 in the females, with frequencies being p_{11} , p_{12} , and p_{22} , respectively. There are two genotypes A_1Y and A_2Y in the males, with frequencies being q_{1y} and q_{2y} , respectively. The sum of all genotypic frequencies equals unity, i.e. $p_{11} + p_{12} + p_{22} + q_{1y} + q_{2y} = 1$. The allele frequencies are p_1 for allele A_1 residing in the females, p_2 for allele A_2 residing in the females, q_1 for allele A_1 residing in the males, q_2 for allele A_2 residing in the males, and q_y for the frequency of the counterpart locus on the Y-chromosome. These allele frequencies can be calculated from genotypic frequencies, i.e. $p_1 = p_{11} + p_{12}/2$, $p_2 = p_{22} + p_{12}/2$, $q_1 = q_{1y}/2$, $q_2 = q_{2y}/2$, and $q_y = q_{1y}/2 + q_{2y}/2$. The secondary sex ratio can be expressed in terms of the genotypic frequencies

$$\lambda_2 = \frac{p_{11} + p_{12} + p_{22}}{q_{1y} + q_{2y}} \tag{1}$$

When there is an equal sum of all genotypic frequencies in the males and females ($p_{11} + p_{12} + p_{22} = q_{1y} + q_{2y}$), an unbiased sex ratio exists ($\lambda_2 = 1$). Eq. (1) can also be rewritten in terms of allele frequencies, i.e. $\lambda_2 = (p_1 + p_2)/(q_1 + q_2 + q_y)$. From this relationship we can obtain $q_1 + q_2 + q_y = (1 + \lambda_2)^{-1}$ and $p_1 + p_2 = \lambda_2(1 + \lambda_2)^{-1}$. Furthermore, we can show that an equal frequency of the X- and Y-chromosomes is present in the males, i.e. $q_y = q_1 + q_2 = 1/(2 + 2\lambda_2)$.

Suppose that a proportion of pollen, denoted by m_p , is replaced with the immigrating pollen grains at the gametophyte stage per generation. Let Q_{1y} and Q_{2y} be the frequencies of genotypes A_1Y and A_2Y in the source population. From the assumptions, let Q_1 , Q_2 , and Q_y be the frequencies of alleles A_1 , A_2 , and the locus (only one allele) on the Y-chromosome, respectively. It can be seen that $Q_1 = Q_{1y}/2$, $Q_2 = Q_{2y}/2$, and $Q_y = Q_{1y}/2 + Q_{2y}/2 = Q_1 + Q_2$. Since only pollen grains can migrate but ovules cannot, the sum of all allele frequencies in the migrating pollen is less than 1, i.e. $Q_1 + Q_2 + Q_y < 1$. Thus, it is necessary to re-scale these frequencies by letting $Q'_1 = Q_1/(Q_1 + Q_2 + Q_y)$, $Q'_2 = Q_2/(Q_1 + Q_2 + Q_y)$, and $Q'_y = Q_y/(Q_1 + Q_2 + Q_y)$ so that $Q'_1 + Q'_2 + Q'_y = 1$. After pollen flow, the allele frequencies in pollen are derived as

$$q_1^* = (1 - m_p)q_1 + \frac{m_p}{1 + \lambda_2} Q'_1, \tag{2a}$$

$$q_2^* = (1 - m_p)q_2 + \frac{m_p}{1 + \lambda_2} Q'_2, \tag{2b}$$

$$q_y^* = (1 - m_p)q_y + \frac{m_p}{1 + \lambda_2} Q'_y. \tag{2c}$$

The expressions $Q'_y = Q'_1 + Q'_2$ and $q_y^* = q_1^* + q_2^*$ remain valid. The allele frequencies in ovules after pollen flow, denoted by p_1^* and p_2^* for alleles A_1 and A_2 , respectively, are the same as in the preceding adults, i.e. $p_1^* = p_1$ and $p_2^* = p_2$. There is no change in both the primary and the secondary sex ratios at this stage ($\lambda_1 = \lambda_2$) since immigration does not alter the relative frequencies of males and females.

Now consider selection at the gametophyte stage. Let the fitness be 1 and $1 - su_2$ for alleles A_1 and A_2 in the ovules, respectively, in which allele A_2 is assumed to be maladaptive; $1 - sv_1$ and $1 - sv_2$ for A_1, A_2 , respectively, in the pollen, and $1 - sv_y$ for the locus on the Y-chromosome. When $v_1 = 0$, the fitness of A_1 in the pollen is the same as its fitness in the ovules. When $sv_y > 0$, the locus on the Y-chromosome has negative effects on the pollen fitness. This may occur when deleterious mutation accumulates due to the absence of recombination between the X- and Y-chromosomes (Fillatov et al., 2000). With these settings, the average fitness at the gametophyte stage is $w_1 = 1 - l_{xx} - l_{xy}$ where l_{xx} and l_{xy} are the migration loads from ovules and pollen, respectively, and they are $l_{xx} = sp_2^*u_2$ and $l_{xy} = s(q_1^*v_1 + q_2^*v_2 + q_y^*v_y)$. After selection at the gametophyte stage, the gamete frequencies are

$$\begin{pmatrix} p_1^{**} \\ p_2^{**} \\ q_1^{**} \\ q_2^{**} \\ q_y^{**} \end{pmatrix} = \frac{1}{w_1} \begin{pmatrix} p_1^* \\ (1 - su_2)p_2^* \\ (1 - sv_1)q_1^* \\ (1 - sv_2)q_2^* \\ (1 - sv_y)q_y^* \end{pmatrix}, \tag{3}$$

where $p_1^{**} + p_2^{**} + q_1^{**} + q_2^{**} + q_y^{**} = 1$.

The primary sex ratio denoted by λ_1^* can be expressed as $\lambda_1^* = (p_1^{**} + p_2^{**}) / (q_1^{**} + q_2^{**} + q_y^{**})$. From Eq. (3), we can obtain

$$\lambda_1^* = \frac{p_1^* + p_2^* - l_{xx}}{q_1^* + q_2^* + q_y^* - l_{xy}} = \frac{\lambda_2(1 - l_{xx}(1 + \lambda_2^{-1}))}{1 - l_{xy}(1 + \lambda_2)}. \tag{4}$$

Note that the relationships $q_1^* + q_2^* + q_y^* = (1 + \lambda_2)^{-1}$ and $p_1^* + p_2^* = \lambda_2(1 + \lambda_2)^{-1}$ are applied in deriving Eq. (4). The primary sex ratio λ_1^* is changed after selection and not the same as the secondary sex ratio λ_2 in the preceding adults. Eq. (4) explicitly indicates that a bias of the primary sex ratio from the secondary sex ratio is related to selection at the gametophyte stage, such as the occurrence of differential pollen competitive abilities or differential ovule abortions.

The genotypic frequencies after combinations between pollen and ovules can be readily obtained. Let p_{11}^*, p_{12}^* , and p_{22}^* be the frequencies of female genotypes A_1A_1, A_1A_2 , and A_2A_2 in seeds, respectively; q_{1y}^* and q_{2y}^* be the frequencies of male genotypes A_1Y and A_2Y in seeds, respectively. These genotypic frequencies can be expressed as $p_{11}^* = p_1^{**}q_1^{**}$, $p_{12}^* = p_1^{**}q_2^{**} + p_2^{**}q_1^{**}$, $p_{22}^* = p_2^{**}q_2^{**}$, $q_{1y}^* = p_1^{**}q_y^{**}$, and $q_{2y}^* = p_2^{**}q_y^{**}$. The sum of all these genotypic frequencies is less than 1, i.e. $p_{11}^* + p_{12}^* + p_{22}^* + q_{1y}^* + q_{2y}^* < 1$. This

arises because only the combinations of pollen with ovules are included and the other combinations such as pollen with pollen and ovules with ovules are not biologically meaningful. These frequencies are rescaled so that their sum equals unity. Let $T = p_{11}^* + p_{12}^* + p_{22}^* + q_{1y}^* + q_{2y}^* = (p_1^{**} + p_2^{**})(q_1^{**} + q_2^{**} + q_y^{**})$. The re-scaled genotypic frequencies are $p'_{11} = p_{11}^*/T$, $p'_{12} = p_{12}^*/T$, $p'_{22} = p_{22}^*/T$, $q'_{1y} = q_{1y}^*/T$, and $q'_{2y} = q_{2y}^*/T$.

Let m_S be the immigration rate of seeds per generation. Thus, the frequencies of these genotypes after seed immigration can be written as

$$p_{ij}^{**} = (1 - m_S)p'_{ij} + m_S P_{ij} \quad (i, j = 1, 2, i \leq j), \tag{5a}$$

$$q_{iy}^{**} = (1 - m_S)q'_{iy} + m_S Q_{iy} \quad (i = 1, 2), \tag{5b}$$

where $P_{11}, P_{12}, P_{22}, Q_{1y}$, and Q_{2y} are the frequencies of genotypes $A_1A_1, A_1A_2, A_2A_2, A_1Y$, and A_2Y in the migrating seeds ($P_{11} + P_{12} + P_{22} + Q_{1y} + Q_{2y} = 1$), respectively. The secondary sex ratio can be altered after seed immigration because the secondary sex ratios in the migrating seeds may be unequal to that in the focal population. The effects of immigrating seeds may be different from the effects of immigrating pollen.

Now consider selection at the sporophyte stage. Let the genotypic fitness be 1 for A_1A_1 , $1 - hsu_{22}$ for A_1A_2 , $1 - su_{22}$ for A_2A_2 , $1 - sv_{1y}$ for A_1Y , and $1 - sv_{2y}$ for A_2Y . The parameter h is the degree of dominance in heterozygotes. When h equals $\frac{1}{2}$, the dominance effect is absent in heterozygote A_1A_2 compared with the fitness of homozygote A_2A_2 . When h is equal to zero, a complete dominance effect is present. When v_{1y} and v_{2y} are unequal, the locus on the Y-chromosome has different effects on the fitness under different backgrounds of the alleles on the X-chromosome. With these settings, the average population fitness is $w_2 = 1 - L_{xx} - L_{xy}$ where $L_{xx} = s(hp_{12}^{**} + p_{22}^{**})u_{22}$, the migration load in the females, and $L_{xy} = s(q_{1y}^{**}v_{1y} + q_{2y}^{**}v_{2y})$, the migration load in the males. After selection at the sporophyte stage, the genotypic frequencies are

$$\begin{pmatrix} p_{11}^{***} \\ p_{12}^{***} \\ p_{22}^{***} \\ q_{1y}^{***} \\ q_{2y}^{***} \end{pmatrix} = \frac{1}{w_2} \begin{pmatrix} p_{11}^{**} \\ (1 - shu_{22})p_{12}^{**} \\ (1 - su_{22})p_{22}^{**} \\ (1 - sv_{1y})q_{1y}^{**} \\ (1 - sv_{2y})q_{2y}^{**} \end{pmatrix}. \tag{6}$$

The secondary sex ratio at the next generation, denoted by λ_2^* , is given by

$$\lambda_2^* = \frac{p_{11}^{***} + p_{12}^{***} + p_{22}^{***}}{q_{1y}^{***} + q_{2y}^{***}} \quad \text{or} \quad \frac{p_1^{***} + p_2^{***}}{q_1^{***} + q_2^{***} + q_y^{***}}, \tag{7}$$

where the allele frequencies are $p_1^{***} = p_{11}^{***} + p_{12}^{***}/2$, $p_2^{***} = p_{22}^{***} + p_{12}^{***}/2$, $q_1^{***} = q_{1y}^{***}/2$, $q_2^{***} = q_{2y}^{***}/2$, and $q_y^{***} = (q_{1y}^{***} + q_{2y}^{***})/2$. The above modeling process, which can be numerically calculated, presents a general situation that can be applied to the case of either strong or weak

selection. In the next section, we assess the analytical relationships between the migration loads and the primary/secondary sex ratios under weak selection.

2.3. Weak selection

Under weak selection, all terms containing the second or higher orders of the selection coefficients (s^2) are small and negligible. The immigration rates of seeds and pollen are assumed to be small as well so that the balance between the effects of migration and selection can be attained. The terms containing the second or higher orders of the immigration rate (m_p^2 , m_s^2 , or $m_s m_p$, or higher orders) or the products of the migration rates and selection coefficients ($s m_p$ or $s m_s$) are neglected.

Under the assumptions mentioned in the above, the migration load at the gametophyte stage is approximated by

$$l_{xy} = s(q_1 v_1 + q_2 v_2 + q_y v_y), \quad (8)$$

which indicates that the migration load is of the order similar to the selection coefficients. The inverse of the average fitness at the gametophyte stage is approximated by

$$\frac{1}{w_1} = 1 + l_{xx} + l_{xy}. \quad (9)$$

From Eq. (3), the sum of all allele frequencies in the females and males is respectively given by

$$\begin{aligned} p_1^{**} + p_2^{**} &= (p_1^* + p_2^*)(1 + l_{xx} + l_{xy}) - l_{xx} \\ &= \frac{1}{1 + \lambda_2}(\lambda_2 - l_{xx} + \lambda_2 l_{xy}), \end{aligned} \quad (10a)$$

$$\begin{aligned} q_1^{**} + q_2^{**} + q_y^{**} &= (q_1^* + q_2^* + q_y^*)(1 + l_{xx} + l_{xy}) - l_{xy} \\ &= \frac{1}{1 + \lambda_2}(1 + l_{xx} - \lambda_2 l_{xy}). \end{aligned} \quad (10b)$$

Thus, the primary sex ratio can be rewritten as

$$\lambda_1^* = \frac{\lambda_2 - l_{xx} + \lambda_2 l_{xy}}{1 + l_{xx} - \lambda_2 l_{xy}}. \quad (11)$$

Eq. (11) gives a clear relationship between the primary and the secondary sex ratios. It can be shown that a biased primary sex ratio is present ($\lambda_1^* \neq 1$) when $\lambda_2 \neq (1 + 2l_{xx}) / (1 + 2l_{xy})$. This expression also reveals that the primary sex ratio is not biased from the secondary sex ratio when selection is absent at the gametophyte stage, irrespective of the differential mortality between the sexes at the sporophyte stage.

The following equations are derived from Eq. (3):

$$q_1^{**} + q_2^{**} = \frac{1}{2(1 + \lambda_2)}(1 + l_{xx} - (1 + 2\lambda_2)l_{xy} + sv_y), \quad (12a)$$

$$q_y^{**} = \frac{1}{2(1 + \lambda_2)}(1 + l_{xx} + l_{xy} - sv_y), \quad (12b)$$

which indicates the expression of $q_y^{**} \neq q_1^{**} + q_2^{**}$ after selection at the gametophyte stage. The sum of allele

frequencies at the locus on the X-chromosome is not the same as that on the Y-chromosome. The relative frequencies of the X- and Y-chromosomes in the male gametes are changed owing to selection at the gametophyte stage.

The inverse value of T used for scaling the genotypic frequencies after random combinations between pollen and ovules is given by

$$\frac{1}{T} = \frac{(1 + \lambda_2)^2}{\lambda_2} \left(1 - (1 - \lambda_2)l_{xx} + \left(\frac{1}{\lambda_2} - 1 \right)l_{xy} \right). \quad (13)$$

Similarly, the inverse average fitness at the sporophyte stage is algebraically simplified as

$$\frac{1}{w_2} = 1 + L_{xx} + L_{xy}. \quad (14)$$

The five genotypic frequencies after selection at the sporophyte stage are approximated by

$$p_{11}^{***} = p_{11}^{**} + \frac{L_{xx} + L_{xy}}{T} p_1^{**} q_1^{**}, \quad (15a)$$

$$p_{12}^{***} = p_{12}^{**} + \frac{L_{xx} + L_{xy} - shu_{22}}{T} (p_1^{**} q_2^{**} + p_2^{**} q_1^{**}), \quad (15b)$$

$$p_{22}^{***} = p_{22}^{**} + \frac{L_{xx} + L_{xy} - su_{22}}{T} p_2^{**} q_2^{**}, \quad (15c)$$

$$q_{1y}^{***} = q_{1y}^{**} + \frac{L_{xx} + L_{xy} - sv_{1y}}{T} p_1^{**} q_y^{**}, \quad (15d)$$

$$q_{2y}^{***} = q_{2y}^{**} + \frac{L_{xx} + L_{xy} - sv_{2y}}{T} p_2^{**} q_y^{**}. \quad (15e)$$

Although the analytical expressions for allele frequencies are difficult to obtain, the relationships between migration load and primary/secondary sex ratio can be derived. Let λ_m be the secondary sex ratio in the migrants that is assumed to be constant in the source populations. Thus, $P_{11} + P_{12} + P_{22} = \lambda_m(1 + \lambda_m)^{-1}$ and $Q_{1y} + Q_{2y} = (1 + \lambda_m)^{-1}$. From Eqs. (7) and (15), the expression for the secondary sex ratio is

$$\lambda_2^* = \frac{c_0 - L_{xx} T^{-1} + m_S \lambda_m (1 + \lambda_m)^{-1}}{c_1 - L_{xy} T^{-1} + m_S (1 + \lambda_m)^{-1}}, \quad (16)$$

where

$$c_0 = (1 - m_S + L_{xx} + L_{xy}) \frac{q_1^{**} + q_2^{**}}{q_1^{**} + q_2^{**} + q_y^{**}}$$

and

$$c_1 = \frac{q_y^{**}}{q_1^{**} + q_2^{**}} c_0.$$

Substituting Eqs. (12) and (13) into (16) yields the recurrent equation for the secondary sex ratio, i.e.

$$\lambda_2^* = \frac{a(1 + \lambda_m) + m_S \lambda_m}{b(1 + \lambda_m) + m_S}, \quad (17)$$

where

$$a = \frac{(1 - m_S + L_{xx} + L_{xy})(1 + l_{xx} - (1 + 2\lambda_2)l_{xy} + sv_y)}{2(1 - \lambda_2 l_{xy} + l_{xx})} - \frac{L_{xx}(1 + \lambda_2)^2}{\lambda_2} \left(1 - (1 - \lambda_2)l_{xx} + \left(\frac{1}{\lambda_2} - 1 \right) l_{xy} \right),$$

and

$$b = \frac{(1 - m_S + L_{xx} + L_{xy})(1 + l_{xx} + l_{xy} - sv_y)}{2(1 - \lambda_2 l_{xy} + l_{xx})} - \frac{L_{xy}(1 + \lambda_2)^2}{\lambda_2} \left(1 - (1 - \lambda_2)l_{xx} + \left(\frac{1}{\lambda_2} - 1 \right) l_{xy} \right).$$

At steady state, the equilibrium equation can be obtained from Eq. (17) by setting $\lambda_2^* = \lambda_2$. With the assumptions mentioned at the beginning of this section, the following cubic equation is obtained:

$$2L_{xy}\lambda_2^3 - \alpha\lambda_2^2 + \beta\lambda_2 - 2L_{xx} = 0, \tag{18}$$

where

$$\alpha = 1 - m_S + 3L_{xx} - L_{xy} + l_{xx} + l_{xy} - sv_y + \frac{2m_S}{1 + \lambda_m},$$

and

$$\beta = 1 - m_S - 3L_{xx} + 3L_{xy} + l_{xx} - l_{xy} + sv_y + \frac{2m_S\lambda_m}{1 + \lambda_m}.$$

The solution to Eq. (18) can be numerically calculated with Mathematica (Wolfram, 1991) when the migration loads at steady state are available. Although the migration rate of pollen is not in Eq. (18), its effects on the secondary sex ratio is realized by changing the allele frequencies and shaping the migration loads at both the gametophyte and sporophyte stages. Substitution of the steady state λ_2 into Eq. (11) gives the primary sex ratio λ_1 at steady state. Next, we examine specific cases involving different combinations of sex and selection and compare the estimates with the exact values calculated from the general model at steady state.

2.3.1. One-sex and one-stage selection

When selection takes place only in the pollen grains, the reduction in population fitness comes from the maladaptive genes in immigrating pollen ($l_{xx} = L_x = L_{xx} = 0$ but $l_{xy} \neq 0$). This can naturally occur in pollen competition for fertilizing ovules (Winsor et al., 2000) or in the genes expressing during pollen-tube growth. From Eqs. (11) and (18), the expressions for the primary and secondary sex ratios at steady state can be simplified (Table 1). It can be seen that $\lambda_1 > \lambda_2$ when $l_{xy} \neq 0$. This can also be viewed from the exact primary sex ratio in Eq. (4) $\lambda_1^* = \lambda_2(1 - l_{xy}(1 + \lambda_2))^{-1} > \lambda_2$. The exact secondary sex ratio (the time-dependent expression; Eq. (7)) is

$$\lambda_2^* = \frac{\chi_1(1 - m_S) + m_S/(1 + \lambda_m)}{(1 - \chi_1)(1 - m_S) + m_S\lambda_m/(1 + \lambda_m)}, \tag{19}$$

where

$$\chi_1 = \frac{(1 - sv_1)q_1^* + (1 - sv_2)q_2^*}{(1 - sv_1)q_1^* + (1 - sv_2)q_2^* + (1 - sv_y)q_y^*}.$$

In the presence of an unbiased sex ratio in the migrants ($\lambda_m = 1$), $\lambda_2^* > 1$ when $sv_y = 1$ (completely detrimental); $\lambda_2^* = 1$ when $sv_y = sv_1 = sv_2 \neq 0$; and $\lambda_2^* < 1$ when $sv_y = 0$ (neutral effects of Y-chromosome).

Numerical results show that the predictions with the approximate equation (Table 1) are slightly higher in comparison with the exact values estimated from the general model at steady state (Section 2.2). Note that in estimating the predicted results with the approximate equations (Table 1), the steady-state migration loads are calculated from the general model. The same patterns can be observed with the change in migration rates of pollen and seeds (e.g., Fig. 2a and b). When the detrimental effect from the Y-chromosome is absent ($sv_y = 0$), a male-biased secondary sex ratio is enhanced, otherwise a female-biased secondary sex ratio is enhanced (Fig. 2a and b).

When selection is only present in the males at the sporophyte stage, migration load exists in the males ($l_{xx} = l_{xy} = L_{xx} = 0$ but $L_{xy} \neq 0$). This case can naturally occur when the heterogametic sex has a higher inviability than the homogametic sex, although few reports are recorded in plants but not in animals (e.g., Haldane’s rule; Haldane, 1922). Under this condition, the primary sex ratio is equal to the secondary sex ratio, i.e. $\lambda_1 = \lambda_2$ at steady state. The expression for the secondary sex ratio at steady state can be simplified from Eq. (18) (Table 1). It is expected that a high inviability in the males can result in a female-biased secondary sex ratio. This can also be inferred from the general model (Section 2.2), i.e.

$$\lambda_2^* = \frac{(1 - m_S)/2 + m_S/(1 + \lambda_m)}{(1 - m_S)/2 + m_S\lambda_m/(1 + \lambda_m) - \chi_2}, \tag{20}$$

where

$$\chi_2 = \frac{1}{2}s(1 - m_S) \left(v_{1y} \frac{p_1^{**}}{p_1^{**} + p_2^{**}} + v_{2y} \frac{p_2^{**}}{p_1^{**} + p_2^{**}} \right) + sm_S(v_{1y}Q_{1y} + v_{2y}Q_{2y}).$$

When $\lambda_m = 1$ and $sv_{1y} \neq 0$ or/and $sv_{2y} \neq 0$, then $\lambda_2^* > 1$. Numerical results show that the female-biased primary or secondary sex ratios are enhanced with an increase in the migration rate of pollen or seeds (Fig. 3). The exact primary/secondary sex ratios are slightly smaller than the predicted values.

When selection is only present in the ovules, the reduction in fitness comes from ovule abortion ($l_{xy} = L_{xy} = L_{xx} = 0$ but $l_{xx} \neq 0$). The immigrating pollen and seeds in the current generation contribute maladaptive alleles to ovules in the next generation. Ovule abortion often occurs, as implied from the observations of the low ratios of seeds to ovules in many plants (Burd, 1994; Melser and Klinkhamer, 2001). The exact primary sex ratio at steady state is $\lambda_1^* = \lambda_2 - (1 + \lambda_2)l_{xx} < \lambda_2$, which is approximated

Table 1
Sex ratios and migration loads under a variety of selection schemes in the presence of an unbiased sex ratio in migrants

Selection	Secondary sex ratio (λ_2)	Primary sex ratio (λ_1)	Migration load
Pollen	$\lambda_2 = \frac{1 - m_S - l_{xy} + sv_y + 2m_S\lambda_m(1 + \lambda_m)^{-1}}{1 - m_S + l_{xy} - sv_y + 2m_S(1 + \lambda_m)^{-1}}$ <p>< 1 (Y-chromosome not detrimental); > 1, otherwise.</p>	$\lambda_1 = \frac{\lambda_2(1 + l_{xy})}{1 - \lambda_2 l_{xy}} > \lambda_2$ <p>$\lambda_1 > \lambda_2$</p>	$l_{xy} \neq 0$
Ovules	$\lambda_2 = \frac{1 - m_S + l_{xx} + 2m_S\lambda_m(1 + \lambda_m)^{-1}}{1 - m_S + l_{xx} + 2m_S(1 + \lambda_m)^{-1}} = 1$	$\lambda_1 = \frac{\lambda_2 - l_{xx}}{1 + l_{xx}} < \lambda_2$	$l_{xx} \neq 0$
Male (sporophyte)	$\lambda_2 = \frac{\alpha \pm \sqrt{\alpha^2 - 8\beta L_{xy}}}{4L_{xy}},$ <p>$\left(\lambda_2 \geq 0; \quad \alpha = 1 - m_S - L_{xy} + \frac{2m_S}{1 + \lambda_m}; \right.$ $\left. \beta = 1 - m_S + 3L_{xy} + \frac{2m_S\lambda_m}{1 + \lambda_m} \right)$ > 1</p>	$\lambda_1 = \lambda_2$	$L_{xy} \neq 0$
Female (sporophyte)	$\lambda_2 = \frac{1 - m_S - 3L_{xx} + 2m_S\lambda_m(1 + \lambda_m)^{-1}}{1 - m_S + 3L_{xx} + 2m_S(1 + \lambda_m)^{-1}} > 1$	$\lambda_1 = \lambda_2$	$L_{xx} \neq 0$
Pollen + male (sporophyte)	$\lambda_2 = \frac{\alpha \pm \sqrt{\alpha^2 - 8\beta L_{xy}}}{4L_{xy}}$ <p>$\left(\lambda_2 \geq 0; \quad \alpha = 1 - m_S - L_{xy} + l_{xy} - sv_y + \frac{2m_S}{1 + \lambda_m}; \right.$ $\left. \beta = 1 - m_S + 3L_{xy} - l_{xy} + sv_y + \frac{2m_S\lambda_m}{1 + \lambda_m} \right)$ > 1</p>	$\lambda_1 = \frac{(1 + l_{xy})\lambda_2}{(1 - \lambda_2 l_{xy})} > \lambda_2$	$l_{xy} \neq 0, L_{xy} \neq 0$
Ovules + female (sporophyte)	$\lambda_2 = \frac{\beta \pm \sqrt{\beta^2 - 8\alpha L_{xx}}}{2\alpha}$ <p>$\left(\lambda_2 \geq 0; \quad \alpha = 1 - m_S + 3L_{xx} + l_{xx} + \frac{2m_S}{1 + \lambda_m}; \right.$ $\left. \beta = 1 - m_S - 3L_{xx} + l_{xx} + \frac{2m_S\lambda_m}{1 + \lambda_m} \right)$ < 1</p>	$\lambda_1 = \frac{\lambda_2 - l_{xx}}{1 + l_{xx}} < \lambda_2$	$l_{xx} \neq 0, L_{xx} \neq 0$
Pollen + ovules	$\lambda_2 = \frac{1 - m_S + l_{xx} + l_{xy} - sv_y + 2m_S(1 + \lambda_m)^{-1}}{1 - m_S + l_{xx} - l_{xy} + sv_y + 2m_S\lambda_m(1 + \lambda_m)^{-1}}$ <p>> 1 (Y-chromosome more detrimental than sex-linked genes); < 1, otherwise.</p>	$\lambda_1 > \frac{1 + l_{xy} - l_{xx}}{1 + l_{xx} - l_{xy}}$ <p>$\lambda_1 < \frac{1 + l_{xy} - l_{xx}}{1 + l_{xx} - l_{xy}}$</p>	$l_{xx} \neq 0, L_{xy} \neq 0$
Male + female (sporophyte)	$2L_{xy}\lambda_2^3 - \alpha\lambda_2^2 + \beta\lambda_2 - 2L_{xx} = 0$ <p>$\left(\alpha = 1 - m_S + 3L_{xx} - L_{xy} + \frac{2m_S}{1 + \lambda_m}; \right.$ $\left. \beta = 1 - m_S - 3L_{xx} + 3L_{xy} + \frac{2m_S\lambda_m}{1 + \lambda_m} \right)$ > 1 (male's selection stronger than female's); < 1, otherwise.</p>	$\lambda_1 = \lambda_2$ <p>$\lambda_1 = \lambda_2$</p>	$L_{xx} \neq 0, L_{xy} \neq 0$
Two-sex + two-stage	Various sex ratios	Various sex ratios	All migration loads exist

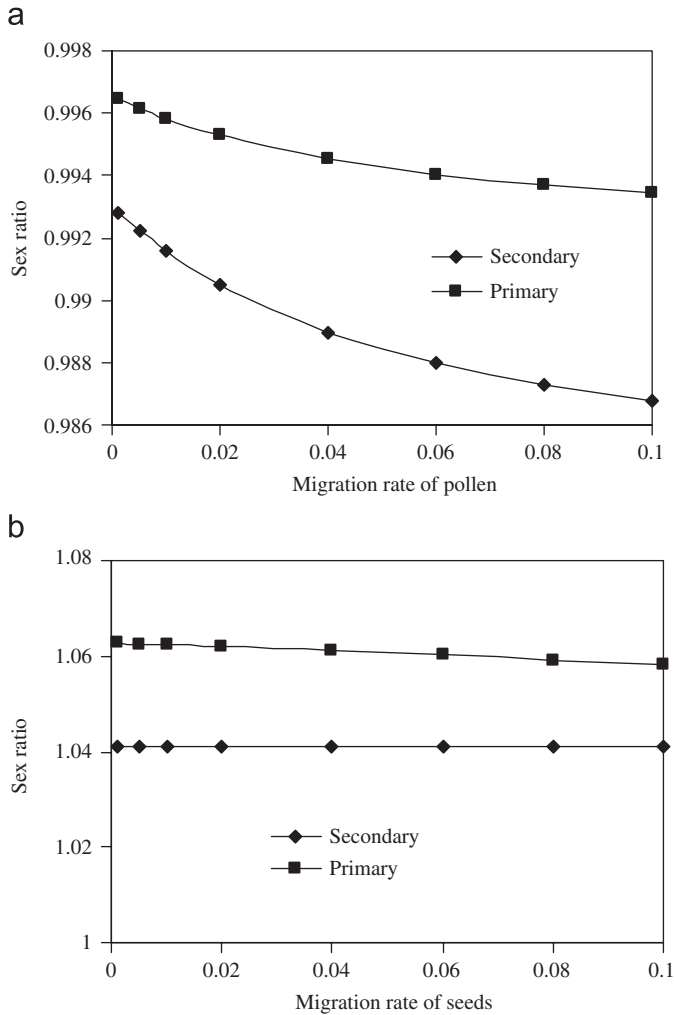


Fig. 2. Effects of the immigrating pollen and seeds on the primary and secondary sex ratios: (a) pollen dispersal and (b) seed dispersal. In (a), the migration rate of seeds is fixed at $m_S = 0.01$, and the other parameters are the selection coefficient of allele A_2 at the gametophyte stage (sv_2) = 0.04 in the pollen and all other selection coefficients = 0. In (b), the immigration rate of pollen is fixed at $m_P = 0.01$, and the other parameters are the selection coefficient of allele A_2 at the gametophyte stage (sv_2) = 0.04 in the pollen, the selection coefficient for the Y-chromosome $s_y = 0.04$, and all other selection coefficients = 0. In each Figure, the frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$ and $Q_{2y} = 0.2$.

by Eq. (11). The simplified expression for the secondary sex ratio at steady state is listed in Table 1. The secondary sex ratio is determined by the sex ratio in migrants (λ_m). When $\lambda_m = 1$, the secondary sex ratio is unbiased ($\lambda_2 = 1$) but the primary sex ratio is male-biased (Fig. 4). The load from the maladaptive genes in the ovules ($l_{xx} \neq 0$) affects the primary sex ratio but does not affect the secondary sex ratio. This is because the secondary sex ratio is determined by the relative frequencies of the X- and Y- chromosomes in the male gametes that are fused with ovules to produce offspring. Although the allele frequencies in the ovules are changed after selection, the secondary sex ratio can be obtained by substituting $\chi_1 = 1/2$ into Eq. (19), i.e. $\lambda_2^* = 1$

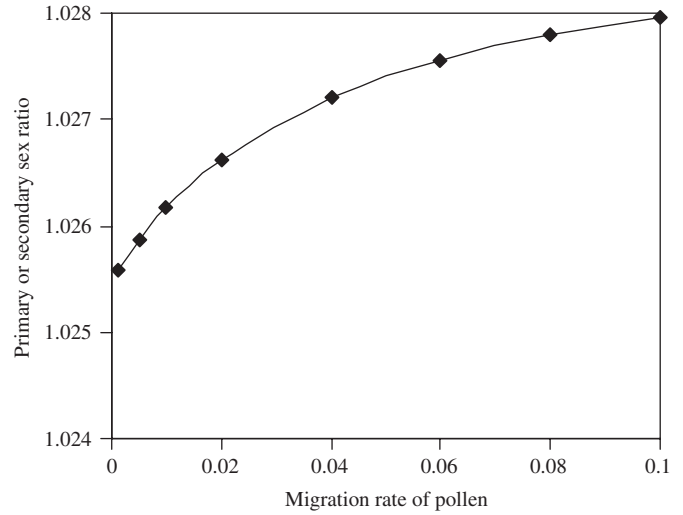


Fig. 3. Effects of the immigrating pollen when selection occurs only in the males at the sporophyte stage. Parameters are the migration rate of seeds fixed at $m_S = 0.01$, and the selection coefficient of allele A_2 at the sporophyte stage $sv_{1y} = 0.02$ and $sv_{2y} = 0.04$, and all other selection coefficients = 0. The frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$ and $Q_{2y} = 0.2$.

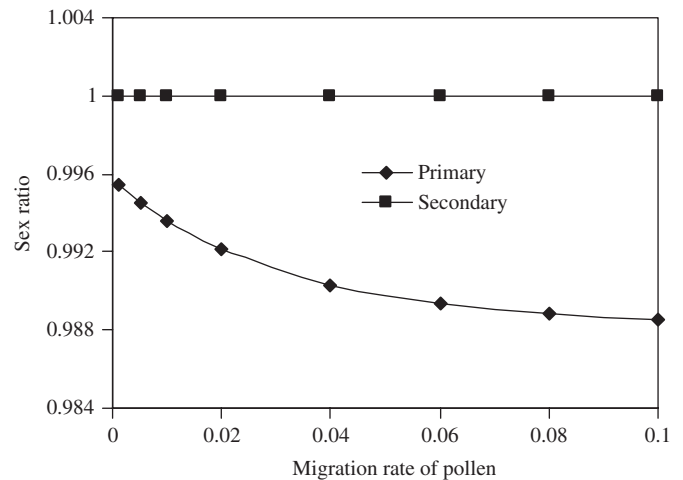


Fig. 4. Effects of the immigrating pollen when selection is only in the females at the gametophyte stage, with the migration rate of seeds fixed at $m_S = 0.01$, the selection coefficient of allele A_2 at the gametophyte stage $sv_2 = 0.04$ and all other selection coefficients = 0. The frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$ and $Q_{2y} = 0.2$.

in the presence of unbiased sex ratio in the immigrants. The exact values calculated from the general model are the same as the predicted values based on the approximate expression in a range of λ_m .

When selection is present only in the females at the sporophyte stage, the reduction in population fitness is due to the maladaptive genes in females ($l_{xy} = l_{xx} = L_{xy} = 0$ but $L_{xx} \neq 0$). The immigrating seeds can directly affect the secondary sex ratio but the immigrating pollen can

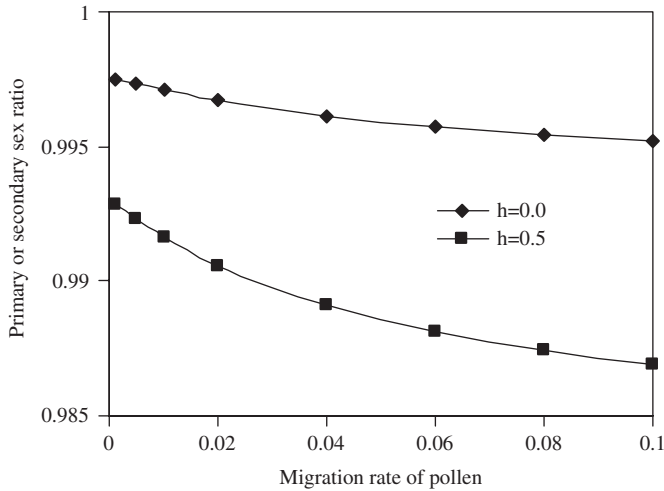


Fig. 5. Effects of the immigrating pollen when selection exists at the sporophyte stage, with the migration rate of seeds fixed at $m_S = 0.01$, the selection coefficient of allele A_2 at the sporophyte stage $su_2 = 0.04$ and all other selection coefficients = 0. The frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$ and $Q_{2y} = 0.2$.

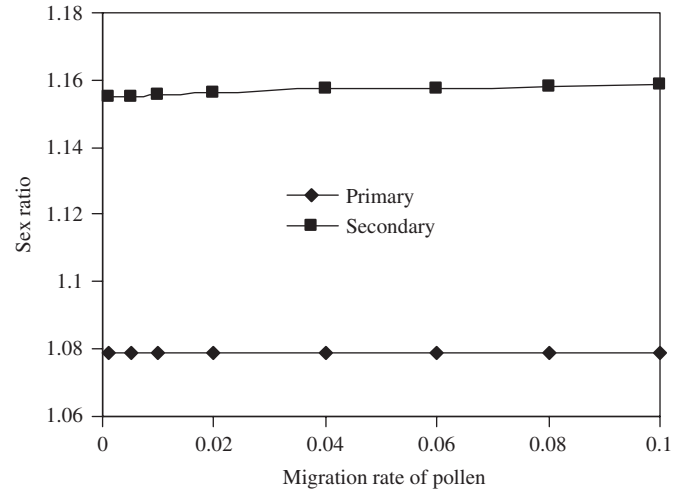


Fig. 6. Effects of the immigrating pollen when selection exists in the pollen and the males at the sporophyte stage, with the migration rate of seeds fixed at $m_S = 0.01$, the selection coefficients $sv_2 = 0.02$, $sv_y = 0.03$, $sv_{1y} = 0.03$, $sv_{2y} = 0.04$, and all other selection coefficients = 0. The frequencies of genotypes in the migrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$ and $Q_{2y} = 0.2$.

indirectly influence the secondary sex ratio through the union with the ovules. This can naturally occur for the females carrying maladaptive genes to retain a lower fertility. The primary sex ratio is equal to the secondary sex ratios at steady state ($\lambda_1 = \lambda_2$). It can be seen from the expression of the secondary sex ratio at steady state (Table 1) that the secondary sex ratio is male-biased ($\lambda_2 < 1$) in the presence of migration loads in the females at the sporophyte stage. The expression from the general model is

$$\lambda_2^* = \frac{(1 - m_S)/2 + m_S/(1 + \lambda_m) - \chi_3}{(1 - m_S)/2 + m_S\lambda_m/(1 + \lambda_m)}, \quad (21)$$

where $\chi_3 = su_{22}(hp_{12}^{**} + p_{22}^{**})$. If $su_{22} \neq 0$ and $\lambda_m = 1$, then $\lambda_2^* < 1$. When the degree of dominance decreases, the migration load increases and the male-biased primary or secondary sex ratios are enhanced (Fig. 5). The secondary sex ratios predicted from approximate equation are slightly lower than the exact values.

2.3.2. One-sex and two-stage selection

Some genes can be expressed at either the gametophyte stage or the sporophyte stage, or both (Charlesworth and Charlesworth, 1992). Many structural genes express in the sporophytic portion of angiosperm life cycle and also experience selection in the pollen (Tanksley et al., 1981; Mulcahy et al., 1996). When selection is present only in the pollen and the males at the sporophyte stage, migration load is present in the males but absent in the females ($l_{xx} = L_{xx} = 0$ but $l_{xy} \neq 0$ and $L_{xy} \neq 0$). The primary sex ratio at steady state is greater than the secondary sex ratio, i.e. $\lambda_1 > \lambda_2$ (Table 1). The purging of maladaptive gametes in the pollen increases the relative frequency of the

female gametes and augments a female-biased primary sex ratio.

Several factors can influence the secondary sex ratio. With an increase in the migration rates of pollen or seeds, the migration loads at both the gametophyte and the sporophyte stages increase, and so are the relative migration loads of l_{xy}/L_{xy} (results not shown here). The secondary sex ratio slightly decreases but the primary sex ratio slightly increases with the migration rates of seeds and pollen (e.g., Fig. 6). A female-biased secondary sex ratio is brought about in the presence of selection in the males and an unbiased sex ratio in the migrants ($\lambda_m = 1$).

When selection is present only in the ovules and the females at the sporophyte stage, migration load is present in the females but absent in the males ($l_{xy} = L_{xy} = 0$ but $l_{xx} \neq 0$ and $L_{xx} \neq 0$). The primary sex ratio at steady state is smaller than the secondary sex ratio, i.e. $\lambda_1 < \lambda_2$ (Table 1). The removal of ovules increases the relative frequency of male gametes and leads to the trend of a male-biased primary sex ratio.

Numerical results show that a male-biased secondary sex ratio is brought about when there is selection in the males and an unbiased sex ratio in the migrants ($\lambda_m = 1$). With an increase in the migration rates of seeds and pollen, the migration loads at both the gametophyte and the sporophyte stages increase but the secondary sex ratio decreases. A negative relationship between l_{xx} and L_{xx} is seen with the change in the degree of dominance. The secondary sex ratio decreases when the degree of dominance decreases. The sex ratios predicted from the approximate equation (Table 1) are slightly lower than the exact values at steady state (results not shown here).

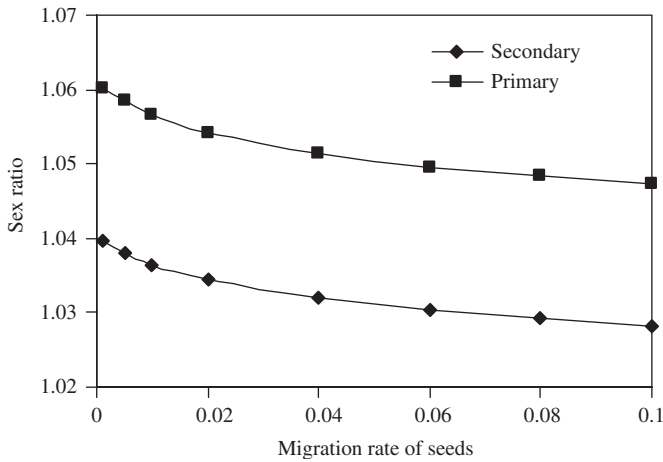


Fig. 7. Effects of the immigrating seeds when selection is present at the gametophyte stage, with the migration rate of pollen $m_P = 0.01$, the selection coefficients $su_2 = 0.02$, $sv_2 = 0.03$, $sv_y = 0.04$, and all other selection coefficients = 0. The frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$.

2.3.3. Two-sex and one-stage selection

When selection is present only in the ovules and pollen, the migration load is absent at the sporophyte stage but present at the gametophyte stage ($L_{xx} = L_{xy} = 0$ but $l_{xx} \neq 0$ and $l_{xy} \neq 0$). This likely occurs in natural populations for the genes that are expressed only in the haploid sage. The primary sex ratio approximated by Eq. (11) can be male- or female-biased, depending upon the relative migration loads of l_{xx} and l_{xy} . In the approximate equation for the secondary sex ratio at steady state (Table 1), the difference between l_{xy} and sv_y at steady state is given by $sv_y - l_{xy} = s(p_1 + p_2)v_y + sq_1(v_y - v_1) + sq_2(v_y - v_2)$. When the locus on the Y-chromosome is detrimental, i.e. $l_{xy} < sv_y$, the female-biased primary and secondary sex ratios are produced owing to a larger load in the pollen (e.g., Fig. 7), which otherwise may produce a male-biased sex ratio. However, both the primary and secondary sex ratios decrease with an increase in the migration rates of pollen and seeds.

In the presence of selection only at the sporophyte stage, the migration load is absent at the gametophyte stage but present at the sporophyte stage ($l_{xx} = l_{xy} = 0$ but $L_{xx} \neq 0$ and $L_{xy} \neq 0$). Differential seed germination and seedling mortality between the males and females in dioecious plants have been documented (Eppley, 2001). The male-biased secondary ratios are partly due to the different post-reproductive growth in many dioecious angiosperms (Lloyd, 1973). The primary sex ratio is equal to the secondary sex ratio ($\lambda_1 = \lambda_2$) since the relative frequencies of male and female gametes are not altered. The secondary sex ratio can be estimated from Eq. (18) with $\alpha = 1 - m_S + 3L_{xx} - L_{xy} + 2m_S/(1 + \lambda_m)$ and $\beta = 1 - m_S - 3L_{xx} + 3L_{xy} + 2m_S\lambda_m/(1 + \lambda_m)$. The results show that a female-biased primary or secondary sex ratio is generated when

selection intensity is greater in the males than in the females, or a male-biased sex ratio is generated when selection intensity is greater in the females than in the males (results not shown here).

2.3.4. Two-sex and two-stage selection

In natural populations, some sex-linked genes can express in both the gametophyte and sporophyte stages (Tanksley et al., 1981; Winsor et al., 2000). The focus here is to study the joint effects of multiple migration loads on the sex ratio on the basis of the general model described in Section 2.1. Only the steady state results are presented here although the transient results are estimated to obtain the steady-state results. The effects of seeds and pollen flow remain the same as those in previous examples on shaping the sex ratio and migration loads (e.g., Fig. 8). The secondary sex ratios predicted from Eq. (18) are slightly

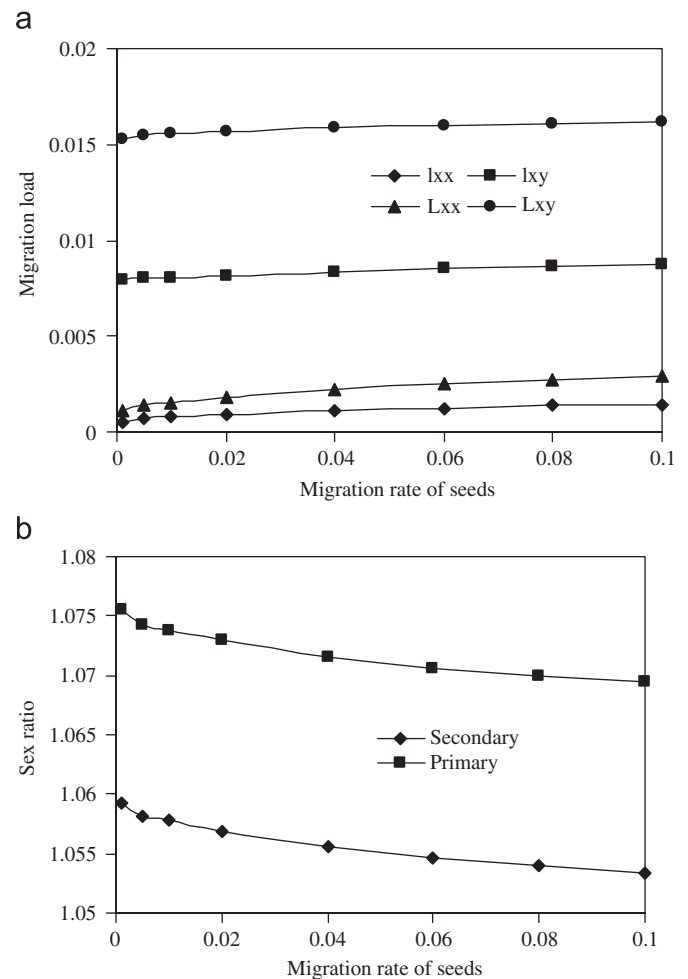


Fig. 8. Effects of the immigrating seeds when selection is present at the gametophyte and sporophyte stages: (a) the migration loads and (b) the primary and secondary sex ratios. The immigration rate of seeds is changed with the immigration rate of pollen fixed at $m_P = 0.01$. Other parameters are the selection coefficients $su_2 = 0.01$, $su_{22} = 0.02$, $sv_{1y} = 0.03$, $sv_{2y} = 0.04$, $sv_y = 0.03$, and $sv_1 = 0.0$. The frequencies of genotypes in the immigrating seeds are $P_{11} = 0.25$, $P_{12} = 0.15$, $P_{22} = 0.1$, $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$. The genotypic frequencies in the immigrating pollen are $Q_{1y} = 0.3$, and $Q_{2y} = 0.2$.

larger than the exact values at steady state. An array of primary and secondary sex ratios can occur under different conditions.

3. Discussion

This study has demonstrated how the maladaptive genes from immigrating seeds and pollen influence the primary and secondary sex ratios in a dioecious plant. The change in the primary and secondary sex ratios can be substantial even when the immigration rates are small. The migration load at the gametophyte stage and/or the sporophyte stage increases with an increasing immigration rate of seeds and pollen, which in turn produces an array of primary and secondary sex ratios. The presence of maladaptive sex-linked genes in the males can enhance the outcome of a female-biased secondary sex ratio, while the presence of maladaptive sex-linked genes in the females or pollen can lead to a male-biased secondary sex ratio. The detrimental effect from the Y-chromosome can generate a female-biased primary or secondary sex ratio. These results highlight the significance of an alternative approach to the existing sex-ratio theories in interpreting the formation of biased sex ratios in a partially isolated population.

It is significant to understand that maladaptive genes can be rapidly eliminated when the focal population is completely isolated from the other populations except under stabilizing selection or when other evolutionary forces counteract the directional selection. Maintenance of maladaptive genes has been examined in theories for population genetics (Wright, 1969) and a species's range (Kirkpatrick and Barton, 1997; Hu and He, 2006). Maladaptive genes should be frequent in plant populations due to the influences from immigrating pollen and seeds in comparison with the effects of deleterious mutation (Mulcahy et al., 1996). In our numerical examples under weak selection (Figs. 2–8), the migration loads at a single locus are about 0.1–2%. The cumulative migration load could be substantial when there are multiple maladaptive loci from immigrating seeds and pollen. The migration load-driven mechanism could be important for interpreting biased sex ratios in plant species with different sex systems, although the present study only addresses the plant species with sexuals determined by the sexual chromosomes. The selection coefficient at the gametophyte stage refers to the relative intensity of selection before the fusion of pollen with ovules, not at a specific time. The selection coefficient at the sporophyte stage refers to the selection intensity from zygote formation to the matured adults. The variation in viability from seed germination to seedling and to adults at the sporophyte stage is not separately considered (Eppley, 2001).

Note that the presence of migration load is dependent on the difference between the frequencies of maladaptive genes in the migrants and recipient population. This result is related to that addressed by Wright (1969, pp. 36–38) for the joint effects of immigration rate and selection except

that the immigration here refers to both seed and pollen dispersal. One caveat is that we have not considered the effects of emigration. In the model of multiple populations such as a finite island model, the exchange of migrants among populations can reduce the variation of gene frequencies in the migrants and recipient populations. The consequence is that the migration load is reduced and the sex ratio is altered.

In comparison with previous non-genetics-based theories of dioecious plants (Bulmer and Taylor, 1980; Charnov, 1982; De Jong et al., 2002), our genetics-based theory accentuates a different biological mechanism. The existing sex-ratio theories for plants are conceptually related to the model of Clark's LRC concept that is originally developed for animal species. Sib mating and LRC are viewed as two important components in the early sex-ratio theories for dioecious plants (De Jong et al., 2002) and the patterns of seeds and pollen dispersal can produce biased secondary sex ratios. The present study does not address the effects of relative distances of seed and pollen dispersal, but emphasizes the relative rates of immigrating seeds and pollen in a focal population. This is fundamentally a different model. Maladaptive genes from immigrating seeds and pollen are important components for producing a biased primary/secondary sex ratio although a small proportion of sib mating occurs due to the assumption of a random combination between pollen and ovules. The LRC model is actually related to the two-stage of selection intensities. A larger selection coefficient is equivalent to a smaller gain of natural resources for the maladaptive gene carriers.

In comparison with the explanations of biased secondary sex ratios from the perspective of life history traits (Delph, 1999), their distinction from the present theory is evident. The effects from immigrating seeds and pollen are not taken into account in the early explanations although plant populations are frequently affected by migrating seeds and pollen that may carry maladaptive genes. Maladaptive genes are maintained by the joint effects of immigration and natural selection. One joint explanation between the present and the life history traits-associated theories is that the difference in first reproduction (the biased primary sex ratio) can bring about a biased secondary sex ratio, which can be explicitly inferred from Eq. (11).

This study assumes that mutation rate is very small and negligible compared with the immigration rates of seed and pollen. This is plausible for the populations with a short history because plants are more influenced by migrants than by deleterious mutants. In the populations with a long history, however, mutation load is likely an important component in reducing population fitness (Charlesworth and Charlesworth, 1992). The mutation load at a single locus is about 2μ where μ is the mutation rate; the mutation load over the whole genome (without epistasis) is about $1 - \exp(-U)$ where U is the sum of total deleterious mutation over the whole genome (Wright, 1977). If U ranges from 0.2 to 2.0 (Lynch and Walsh, 1998), the

mutation load can be substantial, at 18.1–86.5%. Under such a condition, the effects of migration and mutation loads would likely coexist.

The concepts presented here is for individual genes where the interaction among multiple maladaptive genes is excluded. As implied from Hu (2006), the primary and secondary sex ratios may be altered by linkage disequilibria since immigration can generate linkage disequilibrium. Another kind of interaction among multiple genes is the possible effects of sex ratio modifiers that may restore the primary and/or secondary sex ratios to equality (Feldman and Otto, 1989). Under this situation, maintenance of unbiased sex ratios becomes more complicated and the theory that addresses the joint effects of migration load and sex-ratio modifiers is needed.

The present study only addresses the case where sexual dimorphisms are determined by the sexual chromosomes (Ainsworth, 2000; references therein). In plants where sexual is controlled by the autosomal genes, sex determination becomes complicated and multiple loci are often involved (Grant, 1999). In such cases, the relationship between migration load and sex ratio should be assessed.

Numerical applications can be obtained from the theoretical predications concerning the relationships between migration loads and sex ratios. One is to explain the formation of a range of secondary sex ratios in a partially isolated population. In dioecious plants, about 29% of the surveyed species have equal numbers of males and females and 57% have male-biased secondary sex ratios (Lloyd, 1973; Delph, 1999). A few dioecious plants exhibit female-biased secondary sex ratios, such as the species *Rumex nivalis* (Stehlik and Barrett, 2005). Several biological mechanisms were proposed to interpret the underlying processes (Lloyd, 1973; Delph, 1999; Stehlik and Barrett, 2005). An eventual secondary sex ratio can be modified by life history occurrences that cause differential sexual mortality. In reference to the concept presented in this study, these occurrences may occur in the stage of the gametophyte or sporophyte, or in both. With the maladaptive genes from immigrating pollen, the gametophytic selection through differential growth in the pollen tube or ovule abortion can distort the secondary sex ratio. The primary sex ratio (prior to fertilization) is an important reason to cause the secondary sex-ratio distortion (Stehlik and Barrett, 2005), as demonstrated in the present theory. Evidence supporting the secondary sex-ratio distortion from postzygote is widely recorded in the literature. The reduction in population fitness was reported owing to the immigrating seeds and pollen, such as in *Impomopsis aggregate* and *Impatiens capensis* (Burt, 1995). Our results also explicitly show that the differential sexual mortality from the migrating seeds can be an important reason for a partially isolated population.

The second application is to interpret the homogeneity or heterogeneity in the primary/secondary sex ratio among populations that are maintained by the mechanism of gene migration-natural selection. Both the primary and secondary

sex ratios are the function of immigration rates of seeds and pollen and the selection coefficients. The ecological factors that cause the differences in migration rates of seeds and pollen among local populations can result in the variation of population sex ratios in space, such as the shifting of insect pollination to wind pollination (Sakai and Weller, 1999). When there is heterogeneity among populations in purging the maladaptive genes from the immigrating pollen, differential migration loads at the gametophyte stage exist and the spatial variation in the primary/secondary sex ratio evolves. Our results imply that differences in the viability of microgametophytes and megagametophytes among natural populations can confirm our predictions although empirical evidence is rare at the population level. Evidence is also infrequently recorded to show the spatial variation of population sex ratios that is attributable to the differences in removing maladaptive genes from the immigrating seeds, contrast to the case of SSS occurring within populations (Bierzychudek and Eckhart, 1988; Iglesias and Bell, 1989; Korpelainen, 1991; Eppley, 2001; references therein). Thus, empirical studies that examine the spatial migration loads in the males and females would be of particular significance for insights into the spatial pattern of sex ratio at the population level.

The third application of our concept is to interpret the detrimental effects of the Y-chromosome on changing the primary and secondary sex ratios. Since the Y-chromosome does not recombine with its counterpart X-chromosome, the detrimental mutations often accumulate and this in turn increases male mortality (Fllatov et al., 2000). Furthermore, Y-chromosome may have detrimental effects on the X chromosome-linked genes (Charlesworth, 2002), which may take place in the males at the sporophyte stage. The present study provides a choice that is compliant to studying different sets of occurrences in setting different selection coefficients relevant to the Y-chromosome at each stage of the life cycle. Our results indicate that the Y-chromosome can affect the viability of pollen or the viability of males at the sporophyte stage, or both. In each case, the presence of detrimental Y-chromosome from immigrating seeds and pollen can enhance the formation of female-biased primary and secondary sex ratios.

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