Cytonuclear Theory for Haplodiploid Species and X-Linked Genes. I. Hardy-Weinberg Dynamics and Continent-Island, Hybrid Zone Models

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ABSTRACT

We develop models that describe the cytonuclear structure for either a cytoplasmic and nuclear marker in a haplodiploid species or a cytoplasmic and X-linked marker in a diploid species. Sex-specific disequilibrium statistics that summarize nonrandom cytonuclear associations in such systems are defined, and their basic Hardy-Weinberg dynamics and admixture formulae are delimited. We focus on the context of hybrid zones and develop continent-island models whereby individuals from two genetically differentiated source populations migrate into and mate within a single zone of admixture. We examine the effects of differential migration of the sexes, assortative mating by pure type females, and census time (relative to mating and migration), as well as special cases of random mating and migration subsumed under the general models. We show that pure type individuals and nonzero cytonuclear disequilibria can be maintained within a hybrid zone if there is continued migration from both source populations, and that females generally have a greater influence over these cytonuclear variables than males. The resulting theoretical framework can be used to estimate the rates of assortative mating and sex-specific gene flow in hybrid zones and other zones of admixture involving haplodiploid or sex-linked cytonuclear data.

THE study of natural hybrid zones relies heavily on genetic markers and may be greatly aided if both cytoplasmic and nuclear DNA markers are available and assayed in each individual (ARNOLD 1993). The benefit of using such joint data is derived from the fact that cytoplasmic DNA is nearly always inherited uniparentally while nuclear DNA is normally inherited biparentally. As a result, cytonuclear data provide a new and often unique way to detect many evolutionary forces, particularly those that differentially affect the sexes. To take advantage of this novel source of information, models have been developed describing the expected cytonuclear frequencies and disequilibria for autosomal and cytoplasmic markers in diploid species under a variety of evolutionary contexts (CLARK 1984; ASMUSSEN *et al.* 1987, 1989; ARNOLD *et al.* 1988; ASMUSSEN and ARNOLD 1991; ASMUSSEN and SCHNABEL 1991; SCHNABEL and ASMUSSEN 1992; ARNOLD 1993; CELLINO and ARNOLD 1993; BABCOCK and ASMUSSEN 1996). These frameworks have been applied to cytonuclear data to identify zones of admixture and to yield estimates of migration and assortative mating rates of pure parental individuals within a hybrid zone that are more sensitive than, and sometimes unobtainable from, nuclear data alone (ASMUSSEN *et al.* 1989; AVISE *et al.* 1990; SITES *et al.* 1996).

However, the existing models are not adequate for analyzing all types of hybrid zones. For example, they do not address the biologically important situations where females are diploid and males haploid at their nuclear loci, as is the case in haplodiploid species or at X-linked loci in diploid species. In such situations, females inherit their nuclear genes from both parents while males receive their nuclear complement from their mother only. We expect cytonuclear variables to behave differently under these circumstances than under the standard diploid conditions already developed. It is therefore important to delimit this behavior and to determine whether such sex-specific cytonuclear data may be particularly useful and informative in deducing the evolutionary history of natural populations, in the same way that standard cytonuclear data provide a novel way to partition gene flow in plant populations into haploid (pollen) and diploid (seed) components (ASMUSSEN and SCHNABEL 1991; SCHNABEL and ASMUSSEN 1992).

Here, we enlarge the theoretical framework for cytonuclear systems to include models that describe the expected cytonuclear structure for haplodiploid species or X-linked nuclear markers in diploid species. We first define the cytonuclear frequencies and nonrandom associations and analyze their dynamics under basic Hardy-Weinberg conditions, and then we examine the effects of population admixture on the sex-specific cytonuclear disequilibria. This framework is extended to formulate continent-island models of hybridization that incorporate the effects of differential migration of the sexes and assortative mating by females of the two pure parental species. In applying these models to data from

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TABLE 1

Frequencies of joint cytonuclear genotypes in females

	Nuclear genotype			
Cytotype	*AA*	*Aa*	*aa*	Total
C	$u_1 = ux_f + D_1$	$v_1 = vx_f + D_2$	$w_1 = wx_f + D_3$	x_f
c	$u_2 = uy_f - D_1$	$v_2 = vy_f - D_2$	$w_2 = wy_f - D_3$	y_f
Total	u	v	w	1.0

a hybrid zone between two haplodiploid ant species, *Solenopsis invicta* and *S. richteri*, we find the need to further expand this framework to include the cytonuclear effects of population subdivision within the region of hybridization. This subject will be dealt with in a subsequent article.

CYTONUCLEAR VARIABLES

The basic theoretical framework developed here applies equally to data involving an *X*-linked nuclear and cytoplasmic locus in a diploid species, however, for ease of discussion, we will present this in the context of haplodiploids. We assume that there are two alleles (*A*, *a*) at the nuclear locus and two alleles (*C*, *c*) at the haploid, cytoplasmic locus. Variables common to both sexes will be sub- or superscripted by an *m* for males and an *f* for females, while subscripts of *1* or *2* on frequency variables denote cytonuclear combinations with the *C* or *c* cytotype, respectively. For diploid females, the cytonuclear variables are completely analogous to those under the standard diploid cytonuclear formulation (ASMUSSEN *et al.* 1987). The frequencies of the six possible joint genotypes in females are denoted as in Table 1, together with the marginal frequencies of the cytotypes (row sums) and the nuclear genotypes (column sums). From these, we may calculate the nuclear allele frequencies in females as

$$p_f = \text{freq}(A) = u + \tfrac{1}{2}v$$

and

$$q_f = \text{freq}(a) = w + \tfrac{1}{2}v,$$

where $q_f = 1 - p_f$. The remaining female frequency variables are those of the four cytonuclear diallelic combinations (Table 2), which represent the frequencies of female gametes if the cytoplasmic marker is maternally (or biparentally) inherited and no selection occurs. Formally, $p_1^f = \text{freq}(A/C)$, for instance, is defined as the probability that a random female from the population has cytotype *C* and that a randomly sampled allele at her nuclear locus is *A* (ASMUSSEN and BASTEN 1994).

In females, we may define two levels of cytonuclear disequilibria. The first are the genotypic disequilibria,

$$\begin{aligned} D_1 &= \text{freq}(AA/C) - \text{freq}(AA)\text{freq}(C) = u_1 - ux_f \\ D_2 &= \text{freq}(Aa/C) - \text{freq}(Aa)\text{freq}(C) = v_1 - vx_f \\ D_3 &= \text{freq}(aa/C) - \text{freq}(aa)\text{freq}(C) = w_1 - wx_f \end{aligned} \quad (1)$$

that measure the nonrandom association between the cytoplasmic alleles and each female nuclear genotype. We can also define a female allelic disequilibrium,

$$D_f = \text{freq}(A/C) - \text{freq}(A)\text{freq}(C) = p_1^f - p_f x_f, \quad (2)$$

that measures the nonrandom association between the nuclear and cytoplasmic alleles in females, where in both (1) and (2) freq denotes the frequency in females. The female cytonuclear disequilibrium statistics are intimately related by the following equations,

$$D_f = D_1 + \tfrac{1}{2}D_2 \quad \text{and} \quad D_1 + D_2 + D_3 = 0$$

and therefore the four female disequilibria reduce to two independent measures.

Differences between the diploid and haplodiploid models arise when we examine the cytonuclear structure of males. Since males are always haploid at both their nuclear and cytoplasmic loci, there are only four possible male genotypes. Their frequencies, which are analogous to the female diallelic combinations (Table 2), are denoted as in Table 3, along with the marginal

TABLE 2

Frequencies of cytonuclear diallelic combinations in females

	Nuclear allele		
Cytotype	*A*	*a*	Total
C	$p_1^f = u_1 + \tfrac{1}{2}v_1 = p_f x_f + D_f$	$q_1^f = w_1 + \tfrac{1}{2}v_1 = q_f x_f - D_f$	x_f
c	$p_2^f = u_2 + \tfrac{1}{2}v_2 = p_f y_f - D_f$	$q_2^f = w_2 + \tfrac{1}{2}v_2 = q_f y_f + D_f$	y_f
Total	p_f	q_f	1.0

TABLE 3

Frequencies of joint cytonuclear genotypes in males

	Nuclear allele		
Cytotype	A	a	Total
C	$p_1^m = p_m x_m + D_m$	$q_1^m = q_m x_m - D_m$	x_m
c	$p_2^m = p_m y_m - D_m$	$q_2^m = q_m y_m + D_m$	y_m
Total	p_m	q_m	1.0

allele frequencies at the two markers. Males have the single, allelic disequilibrium defined as

$$D_m = \text{freq}(A/C) - \text{freq}(A)\text{freq}(C) = p_1^m - p_m x_m, \quad (3)$$

where freq now denotes the frequency in males. This statistic is analogous to, but distinct from, the female measure D_f in (2). The frequencies of the male genotypes and the female cytonuclear combinations can be written in terms of the relevant sex-specific disequilibria and marginal nuclear and cytotype frequencies as shown in Tables 1–3.

BASIC CYTONUCLEAR DYNAMICS

We first analyze the baseline dynamical behavior of this haplodiploid (and *X*-linked) cytonuclear system under Hardy-Weinberg conditions. We assume random mating and no selection or input of new alleles through mutation or migration. Population size is large enough to preclude the effects of drift, and generations are discrete and nonoverlapping. A female is diploid and assumed to obtain half of her nuclear complement from her mother and half from her father; however, her cytoplasmic allele is assumed to be strictly inherited through her mother. Males receive their sole allele at each nuclear and cytoplasmic locus from their mother.

We begin by deriving the female cytonuclear dynamics. Through analysis of a mating table we find that after one generation of mating the frequencies of the joint cytonuclear genotypes in females are

$$u_i' = p_i^f p_m \quad v_i' = p_i^f q_m + q_i^f p_m \quad w_i' = q_i^f q_m \quad (4)$$

for $i = 1, 2$, where a prime ($'$) indicates the value in the new generation. We see that the form of these equations clearly delimits the maternal and paternal contributions to each female genotypic class. For example, an AA/C individual is produced by receiving an A/C diallelic combination from the female gamete pool (with probability p_1^f) and an A allele from the male gamete pool (with probability p_m). By summing (4) over the two cytotypes, we find the new marginal nuclear genotype frequencies to be

$$u' = p_f p_m \quad v' = p_f q_m + q_f p_m \quad w' = q_f q_m, \quad (5)$$

while the new nuclear and cytoplasmic allele frequencies in females are

$$p_f' = \tfrac{1}{2}(p_f + p_m) \quad x_f' = x_f. \quad (6)$$

As expected, the nuclear frequencies follow the standard Hardy-Weinberg dynamics for haplodiploids (and *X*-linked loci), since the nuclear genes are assumed to assort independently of the cytotype marker. In contrast, the cytotype frequency in females does not change from its initial value since males do not contribute alleles to the cytoplasmic gene pool, and females are haploid at their cytoplasmic locus.

We may now use the female frequency recursions from (4) to (6) in conjunction with (1) and (2) to show that the genotypic and allelic disequilibria in females are changed by random mating to

$$\begin{aligned} D_1' &= p_m D_f \\ D_2' &= (q_m - p_m) D_f \\ D_3' &= -q_m D_f \\ D_f' &= \tfrac{1}{2} D_f. \end{aligned} \quad (7)$$

We see that the recursions for the female disequilibria in the haplodiploid model are determined by the nuclear allele frequencies in the male gamete pool (p_m, q_m) and the allelic disequilibrium in the female gamete pool (D_f), and are identical to those in the standard, diploid cytonuclear model when there are frequency differences between the sexes (Babcock and Asmussen 1996). Moreover, D_f decays at the same rate as the gametic phase disequilibrium between two unlinked nuclear loci (Hartl and Clark 1989).

The frequencies of the four male genotypes in the next generation are given by the corresponding female diallelic combinations in the previous generation,

$$(p_i^m)' = p_i^f \quad (q_i^m)' = q_i^f \quad (8)$$

for $i = 1, 2$, and consequently the new allele frequencies and allelic disequilibrium in males are also a direct reflection of those in their mothers,

$$p_m' = p_f \quad x_m' = x_f \quad D_m' = D_f. \quad (9)$$

The male and female recursions can be used to solve for the time-dependent solutions for the allele frequencies and disequilibria in both sexes, which, via the marginal recursions in (5) and relationships given in Tables 1–3, completely define the cytonuclear dynamics in the population. To derive these dynamical solutions, define $z^{(t)}$ as the value of the variable z in any generation t and $z^{(0)}$ as the initial value of z. If we further define the initial, overall nuclear allele frequency in the population as $p = \frac{2}{3}p_f^{(0)} + \frac{1}{3}p_m^{(0)}$, and the initial difference in the nuclear allele frequencies in females and males as $\Delta^{(0)} = p_f^{(0)} - p_m^{(0)}$, then the nuclear allele frequencies

in males and females in any generation, $t = 0, 1, 2, \ldots$, are given by

$$p_f^{(t)} = p + \tfrac{1}{3}\Delta^{(0)}(-\tfrac{1}{2})^t$$
$$p_m^{(t)} = p_f^{(t-1)} = p - \tfrac{2}{3}\Delta^{(0)}(-\tfrac{1}{2})^t. \qquad (10)$$

These follow the standard Hardy-Weinberg dynamics for haplodiploid (or *X*-linked) loci (HARTL and CLARK 1989), under which p_f and p_m both approach the constant, overall nuclear allele frequency, p, in a damped oscillatory fashion. After the first generation, the male cytotype frequency takes on the frequency in females, and thereafter the cytotype frequencies in both sexes remain at the initial value in females, so that

$$x_f^{(t)} \equiv x_m^{(t)} \equiv x_f^{(0)}$$

for $t = 1, 2, \ldots$. Using the nuclear allele frequency dynamics in (10) and the recursions for the cytonuclear disequilibrium statistics in (7) and (9), we can next solve for the values of the four disequilibria at any time t, which are given by

$$D_1^{(t)} = [p(\tfrac{1}{2})^{t-1} - \tfrac{2}{3}\Delta^{(0)}(-\tfrac{1}{4})^{t-1}]D_f^{(0)}$$
$$D_2^{(t)} = [(q - p)(\tfrac{1}{2})^{t-1} + \tfrac{4}{3}\Delta^{(0)}(-\tfrac{1}{4})^{t-1}]D_f^{(0)}$$
$$D_3^{(t)} = -[q(\tfrac{1}{2})^{t-1} + \tfrac{2}{3}\Delta^{(0)}(-\tfrac{1}{4})^{t-1}]D_f^{(0)}$$
$$D_f^{(t)} = D_f^{(0)}(\tfrac{1}{2})^t$$
$$D_m^{(t)} = D_f^{(t-1)} = D_f^{(0)}(\tfrac{1}{2})^{t-1}.$$

As in the standard diploid model (ASMUSSEN *et al.* 1987), all disequilibria rapidly decay to zero, and within six generations, all of the values will be below 0.01 in magnitude, which represents a minimum detectable level for reasonable sample sizes and marginal allele frequencies (ASMUSSEN and BASTEN 1994). The female allelic disequilibrium, D_f, decays monotonically with no change in sign, and after the first generation the male disequilibrium, D_m, assumes twice the value of D_f, lagging one generation behind. In females, the homozygote genotypic disequilibrium, D_1, takes on and retains the sign of the female allelic disequilibrium, while D_3 takes the opposite sign of D_f. Interesting disequilibrium dynamics, not found in the standard diploid model, are possible if initially there are nuclear allele frequency differences between the sexes ($p_f^{(0)} \neq p_m^{(0)}$) and nonrandom allelic associations in females ($D_f^{(0)} \neq 0$). In particular, under these conditions, it is possible for the female genotypic disequilibria to increase in magnitude past the first generation. Furthermore, the values of both homozygote disequilibria, D_1 and D_3, may oscillate in the initial generations as a result of nuclear allele frequency oscillations, but these disequilibria eventually decay monotonically to zero as the nuclear allele frequency equilibrates in the two sexes. Like the homozygote disequilibria, the magnitude of the heterozygote disequilibrium, D_2, will also ultimately decay monotonically, but the sign of D_2 may exhibit permanent cycling

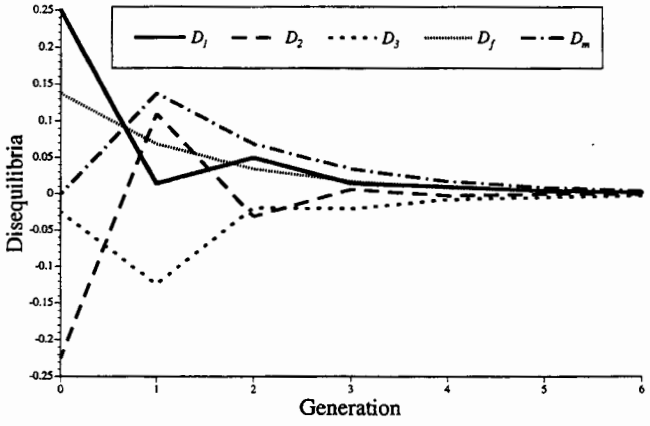

FIGURE 1.—Cytonuclear disequilibria under Hardy-Weinberg conditions for the initial frequencies: $u_1 = 0.5$, $v_1 = w_1 = u_2 = 0$, $v_2 = 0.45$, $w_2 = 0.05$; $p_1^m = 0.1$, $q_1^m = 0.9$, $p_2^m = q_2^m = 0$.

if initially the overall nuclear allele frequency (p) is 0.5 and the initial nuclear allele frequencies in the sexes differ ($p_f^{(0)} \neq p_m^{(0)}$). An example of the dynamical behavior of the sex-specific disequilibria is illustrated in Figure 1.

POPULATION ADMIXTURE

Pooling genetically differentiated populations can generate both nuclear and cytonuclear disequilibria in diploid species (NEI and LI 1973; ASMUSSEN and ARNOLD 1991), and we expect similar effects on cytonuclear disequilibria involving haplodiploid species or *X*-linked loci. Consider the general case where n distinct populations are combined into a single population. Define the mean value of the variable z across all n populations as

$$\bar{z} = \sum_{i=1}^{n} m_i z^{(i)}, \qquad (11)$$

where m_i is the fraction from subpopulation i and $z^{(i)}$ is the value of variable z in subpopulation i. Then, from (2) and (11) the female allelic disequilibrium in the pooled population is

$$D_f^T = \overline{p_1^f} - \bar{p}_f\bar{x}_f$$
$$= \overline{p_1^f} - \overline{p_f x_f} + \mathrm{cov}(p_f, x_f)$$
$$= \bar{D}_f + \mathrm{cov}(p_f, x_f).$$

Similar calculations for the female genotypic disequilibria, D_i, and male allelic disequilibrium, D_m, show that in the combined population

$$D_i^T = \bar{D}_i + \mathrm{cov}(g_i, x_f) \quad D_m^T = \bar{D}_m + \mathrm{cov}(p_m, x_m),$$

where $g_i = u$, v, or w for $i = 1, 2, 3$, respectively. These results mirror those found under the standard diploid formulation, in that each total disequilibrium is the weighted average of the values in the subpopulations plus the covariance between the cytotype frequency and

the appropriate nuclear frequency across the subpopulations (ASMUSSEN and ARNOLD 1991). The covariance terms have a particularly nice interpretation in the special case when just two subpopulations are pooled, for which the admixture formulas become

$$D_i^T = \bar{D}_i + m_1(1 - m_1)(g_i^{(1)} - g_i^{(2)})(x_f^{(1)} - x_f^{(2)})$$
$$D_f^T = \bar{D}_f + m_1(1 - m_1)(p_f^{(1)} - p_f^{(2)})(x_f^{(1)} - x_f^{(2)})$$
$$D_m^T = \bar{D}_m + m_1(1 - m_1)(p_m^{(1)} - p_m^{(2)})(x_m^{(1)} - x_m^{(2)}), \quad (12)$$

where, once again, $g_i = u$, v, or w for $i = 1, 2, 3$, respectively. In this instance, the covariances are nonzero, and there is a cytonuclear admixture effect in that the total disequilibrium differs from the mean of the values in the subpopulations, if and only if the cytotype and the associated nuclear frequency both differ across the two subpopulations. In general, to have an admixture effect with more than two subpopulations, it is necessary but not sufficient that both the nuclear and cytoplasmic components vary across subpopulations.

CONTINENT-ISLAND MODELS FOR HAPLODIPLOIDS

In this section we develop models that explore the effects of hybridization on the cytonuclear structure of haplodiploid species. We assume that individuals from two genetically differentiated populations continuously migrate into a zone of admixture where mating occurs. Although our model is more general, we are primarily interested in hybrid zones where the source populations are fixed for alternate alleles. In this case, source population 1 (species 1) will be composed only of females of genotype AA/C and males of genotype A/C, while source population 2 (species 2) is composed only of females of genotype aa/c and males of genotype a/c. In the hybrid zone, individuals who possess two-locus homospecific allelic combinations may either be pure parental individuals or hybrids that look like pure parental individuals at the two-locus level. As in previous diploid formulations (ARNOLD *et al.* 1988; ASMUSSEN *et al.* 1989), it is useful to divide these homoallelic classes into subclasses based on their true species status. Females that display genotype AA/C, for example, may either be pure parentals from source population 1 (freq u_{1s}), or they may be hybrids (freq u_{1h}). We may subdivide the other homoallelic classes in similar ways to obtain the four partitions,

$$u_1 = u_{1s} + u_{1h} \quad w_2 = w_{2s} + w_{2h}$$
$$p_1^m = p_{1s}^m + p_{1h}^m \quad q_2^m = q_{2s}^m + q_{2h}^m,$$

where the subscript s represents a pure species individual and the subscript h represents a hybrid. In practice, these subclasses may be distinguished from one another with a high degree of confidence through the examination of multiple diagnostic nuclear loci in conjunction with a diagnostic cytoplasmic marker.

Interestingly, the dynamics of the pure species individuals in the haplodiploid and the diploid, *X*-linked models deviate due to the differing modes of male production. Haplodiploid males are produced parthenogenetically; therefore all the sons of a pure type female will be pure type males. This is not true in the diploid case where a pure species son is produced if and only if a pure species female mates with a conspecific male (since all sexually produced sons receive half their autosomal complement from their father, which, although not monitored, nonetheless affect their true species status). Pure type females are not affected in this way since in both the haplodiploid and *X*-linked cases they can only be produced through the union of a pure type female and male. In this section we will focus on the case of haplodiploids. The differences that arise when considering an *X*-linked marker in a diploid species will be dealt with in the CONTINENT-ISLAND MODELS FOR *X*-LINKED LOCI section below.

As in previous formulations (ASMUSSEN *et al.* 1989), our continent-island model incorporates assortative mating within the hybrid zone by assuming that a pure species 1 female will preferentially mate with a conspecific male with probability α and mate at random with probability $1 - \alpha$. Similarly, a pure species 2 female will preferentially mate with a conspecific male with probability β and mate at random with probability $1 - \beta$. The other six, hybrid type females are assumed to always mate at random. Our formulation includes random mating as a special case corresponding to $\alpha = \beta = 0$ (see below).

We assume that every generation a constant fraction, $m_f^{(1)}$, of females within the hybrid zone are migrants from source population 1, and a constant fraction, $m_f^{(2)}$, of females are migrants from source population 2, while the remaining fraction of females, $1 - m_f^{(1)} - m_f^{(2)}$, are offspring of previous residents. Males may migrate into the hybrid zone at different rates from the females so that every generation, a fraction $m_m^{(1)}$ and $m_m^{(2)}$ of the males are migrants from source populations 1 and 2, respectively, with the remaining fraction of males produced by females already in the hybrid zone. We denote the overall values of the cytonuclear variables in the male and female migrant pools as $\bar{p}_f$, $\bar{p}_m$, $\bar{x}_f$, $\bar{u}_1$, $\bar{p}_1^m$, $\bar{D}_f$, etc. For all frequencies this overall value is simply the arithmetic average of the corresponding frequencies in the two source populations weighted by the appropriate sex-specific migration rate. For example, if the cytotype frequency in females is $x_f^{(1)}$ and $x_f^{(2)}$ in source populations 1 and 2, respectively, then the female cytotype frequency in the migrants is $\bar{x}_f = (m_f^{(1)}x_f^{(1)} + m_f^{(2)}x_f^{(2)})/(m_f^{(1)} + m_f^{(2)})$. The cytonuclear disequilibria in the migrant pools can be computed from their definitions (e.g., $\bar{D}_1 = \bar{u}_1 - \bar{u}\,\bar{x}_f$) or from the admixture formulae in (12). In the special case of interest, where the two source populations are fixed for alternate alleles, the frequencies and disequilibria in the

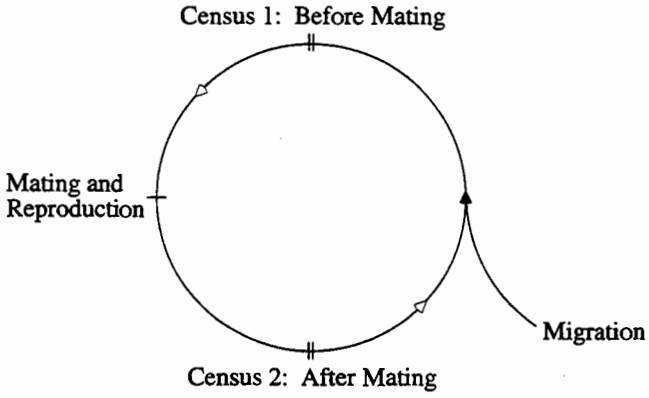

FIGURE 2.—Census times of individuals within hybrid zones. Censusing may occur before mating and after migration (census 1) or before migration and after mating (census 2).

migrants are simple functions of the sex-specific migration rates, with

$$\begin{aligned}
\bar{u}_{1s} &= \bar{u}_1 = \bar{p}_f = \bar{x}_f = m_f^{(1)}/m_f \\
\bar{w}_{2s} &= \bar{w}_2 = \bar{q}_f = \bar{y}_f = m_f^{(2)}/m_f \\
\bar{u}_{1h} &= \bar{v}_1 = \bar{w}_1 = \bar{u}_2 = \bar{v}_2 = \bar{w}_{2h} = \bar{D}_2 = 0 \\
\bar{D}_f &= \bar{D}_1 = -\bar{D}_8 = m_f^{(1)} m_f^{(2)}/(m_f)^2
\end{aligned} \tag{13}$$

in females, where $m_f = m_f^{(1)} + m_f^{(2)}$, is the total female migration rate, and

$$\begin{aligned}
\bar{p}_{1s}^m &= \bar{p}_1^m = \bar{p}_m = \bar{x}_m = m_m^{(1)}/m_m \\
\bar{q}_{2s}^m &= \bar{q}_2^m = \bar{q}_m = \bar{y}_m = m_m^{(2)}/m_m \\
\bar{p}_{1h}^m &= \bar{p}_2^m = \bar{q}_1^m = \bar{q}_{2h}^m = 0 \\
\bar{D}_m &= m_m^{(1)} m_m^{(2)}/(m_m)^2
\end{aligned} \tag{14}$$

in males, where $m_m = m_m^{(1)} + m_m^{(2)}$ is the total male migration rate. Although we are specifically interested in zones of hybridization between two genetically distinct species, we need only modify the cytonuclear frequencies and disequilibria in the migrants, given by (13)–(14), to make our model applicable to any population receiving unidirectional gene flow from any number of sources with arbitrary compositions. Except for the continuous migration and potential for assortative mating, the monitored population satisfies the Hardy-Weinberg conditions specified in the BASIC CYTONUCLEAR DYNAMICS section.

Model with censusing after migration and before mating (census 1)

As in the standard diploid formulation (ASMUSSEN *et al.* 1989), the values of cytonuclear variables in the haplodiploid model differ with the timing of censusing relative to mating and migration (Figure 2). Here we develop the model for censusing before mating and after migration of individuals into the hybrid zone (census 1). The alternative framework (census 2) and the consequences of censusing time will be discussed below.

Female recursions: We first turn our attention to the dynamics of the female cytonuclear variables under census 1. In contrast to the standard diploid model (ASMUSSEN *et al.* 1989), the female genotypic recursions in the haplodiploid model reveal the explicit contribution of males and females to the next generation. Each female frequency variable is the weighted average of the corresponding value in migrant females and the female progeny of the previous residents, weighted by the total female migration rate, m_f. Through analysis of a mating table, it can be shown that the resulting recursions for the two parental female classes are

$$\begin{aligned}
u'_{1s} &= m_f \bar{u}_{1s} + (1 - m_f) u_{1s}[\alpha + (1 - \alpha) p_{1s}^m] \\
w'_{2s} &= m_f \bar{w}_{2s} + (1 - m_f) w_{2s}[\beta + (1 - \beta) q_{2s}^m],
\end{aligned} \tag{15}$$

while those for the six basic female cytonuclear genotypes are

$$\begin{aligned}
u'_1 &= m_f \bar{u}_1 + (1 - m_f)[p_m(p_f x_f + D_f) + \alpha u_{1s} q_m] \\
v'_1 &= m_f \bar{v}_1 + (1 - m_f)[(p_f q_m + q_f p_m) x_f \\
&\quad + (q_m - p_m) D_f - \alpha u_{1s} q_m] \\
w'_1 &= m_f \bar{w}_1 + (1 - m_f) q_m (q_f x_f - D_f) \\
u'_2 &= m_f \bar{u}_2 + (1 - m_f) p_m (p_f y_f - D_f) \\
v'_2 &= m_f \bar{v}_2 + (1 - m_f)[(p_f q_m + q_f p_m) y_f \\
&\quad - (q_m - p_m) D_f - \beta w_{2s} p_m] \\
w'_2 &= m_f \bar{w}_2 + (1 - m_f)[q_m(q_f y_f + D_f) + \beta w_{2s} p_m].
\end{aligned} \tag{16}$$

For ease of analysis, we have expressed the female recursions in terms of the basic cytonuclear variables (pure species frequencies, allele frequencies, and female allelic disequilibrium); however, they are more readily derived in terms of the female diallelic combinations (*e.g.*, the new frequency of the AA/C genotype is $u'_1 = m_f \bar{u}_1 + (1 - m_f)[p_f^2 p_m + \alpha u_{1s} q_m]$). From the joint genotypic recursions in (16), we find that the new marginal nuclear genotype frequencies in females become

$$\begin{aligned}
u' &= m_f \bar{u} + (1 - m_f)(p_f p_m + \alpha u_{1s} q_m) \\
v' &= m_f \bar{v} + (1 - m_f)(p_f q_m + q_f p_m - \alpha u_{1s} q_m - \beta w_{2s} p_m) \\
w' &= m_f \bar{w} + (1 - m_f)(q_f q_m + \beta w_{2s} p_m)
\end{aligned} \tag{17}$$

and the new female allele frequencies are thus

$$\begin{aligned}
p'_f &= m_f \bar{p}_f + \tfrac{1}{2}(1 - m_f)(p_f + p_m + \alpha u_{1s} q_m - \beta w_{2s} p_m) \\
x'_f &= m_f \bar{x}_f + (1 - m_f) x_f.
\end{aligned} \tag{18}$$

In females, only the cytotype frequency is both completely independent of male variables and unaffected by assortative mating.

The new values of the four female cytonuclear dis-

equilibria can be computed directly from their definitions in (1)–(2) and the frequency recursions given in (16)–(18) and represent the result of admixture between migrant females and the female progeny of the residents in the previous generation,

$$D_1' = m_f\bar{D}_1 + (1 - m_f)(p_m D_f + \alpha u_{1s} q_m y_f) + m_f(1 - m_f)(p_f p_m + \alpha u_{1s} q_m - \bar{u})(x_f - \bar{x}_f) \quad (19a)$$

$$D_2' = m_f\bar{D}_2 + (1 - m_f)[(q_m - p_m)D_f - \alpha u_{1s} q_m y_f + \beta w_{2s} p_m x_f] + m_f(1 - m_f)(p_f q_m + q_f p_m - \alpha u_{1s} q_m - \beta w_{2s} p_m - \bar{v})(x_f - \bar{x}_f) \quad (19b)$$

$$D_3' = m_f\bar{D}_3 - (1 - m_f)(q_m D_f + \beta w_{2s} p_m x_f) + m_f(1 - m_f)(q_f q_m + \beta w_{2s} p_m - \bar{w})(x_f - \bar{x}_f) \quad (19c)$$

$$D_f' = m_f\bar{D}_f + \tfrac{1}{2}(1 - m_f)(D_f + \alpha u_{1s} q_m y_f + \beta w_{2s} p_m x_f) + \tfrac{1}{2}m_f(1 - m_f)(p_f + p_m + \alpha u_{1s} q_m - \beta w_{2s} p_m - 2\bar{p}_f)(x_f - \bar{x}_f). \quad (19d)$$

As in the standard diploid formulation (ASMUSSEN *et al.* 1989), the new female disequilibrium values are thus each composed of three terms. Here, the first two of these represent the weighted average of the disequilibria in the female migrant pool and in the female progeny of the previous residents of the hybrid zone, while the final term represents the admixture effect caused by nuclear and cytoplasmic frequency differences between these two groups.

Male recursions: Males are unaffected by assortative mating since they are produced asexually. Their frequencies in the next generation are simply the weighted averages of the values in the migrant males and the corresponding values in the previous resident females, weighted by the total male migration rate. The recursions for the male genotypic frequencies are thus

$$\begin{aligned}(p_{1s}^m)' &= m_m\bar{p}_{1s}^m + (1 - m_m)u_{1s}\\ (q_{2s}^m)' &= m_m\bar{q}_{2s}^m + (1 - m_m)w_{2s}\\ (p_i^m)' &= m_m\bar{p}_i^m + (1 - m_m)p_i^f\\ (q_i^m)' &= m_m\bar{q}_i^m + (1 - m_m)q_i^f\end{aligned} \quad (20)$$

for $i = 1, 2$, while the male allele frequency recursions are

$$p_m' = m_m\bar{p}_m + (1 - m_m)p_f \quad x_m' = m_m\bar{x}_m + (1 - m_m)x_f.$$

Admixture has a more complicated effect on the male allelic disequilibrium in the next generation so that,

$$D_m' = m_m\bar{D}_m + (1 - m_m)D_f + m_m(1 - m_m)(p_f - \bar{p}_m)(x_f - \bar{x}_m). \quad (21)$$

As in females, the new male disequilibrium is composed of three terms. The first two terms parallel the male frequency recursions and are weighted averages of the allelic disequilibrium in the male migrant pool and the resident females of the previous generation, while the third term represents the male admixture effect that is generated by frequency differences between migrant males and resident females.

Equilibrium state: There is a unique, joint equilibrium for this haplodiploid cytonuclear system with $0 < \hat{u}_{1s}, \hat{w}_{2s}, \hat{p}_{1s}^m, \hat{q}_{2s}^m < 1$ if $0 < m_f, \bar{u}_{1s}, \bar{w}_{2s} < 1$ and $0 \leq \alpha, \beta, m_m < 1$, and this equilibrium can be shown to be locally stable whenever it exists (see APPENDIX A). The equilibrium frequencies of the pure parental females, $\hat{u}_{1s}$ and $\hat{w}_{2s}$, are each obtained as the root of a quadratic equation and their derivations are provided in APPENDIX B. From these, the steady-state frequencies of the pure parental, haploid males, $\hat{p}_{1s}^m$ and $\hat{q}_{2s}^m$, are then simply obtained from the (recursion) relationships in (20). We find that, as in the standard, diploid formulation (ASMUSSEN *et al.* 1989), $\hat{u}_{1s} < \bar{u}_{1s}$ and $\hat{w}_{2s} < \bar{w}_{2s}$. That is, the frequency of pure parental females in the hybrid zone must always be less than that in the female migrant pool. Interestingly, the corresponding relationship does not necessarily hold for pure species males, whose equilibrium frequency can exceed that in male migrants if, in the migrants, the frequency of pure species females exceeds that of pure species males (*e.g.*, $\hat{p}_{1s}^m$ can exceed $\bar{p}_{1s}^m$ if $\bar{u}_{1s} > \bar{p}_{1s}^m$). Derivations of these pure species results can be found in APPENDIX B.

The only variables for which the full time-dependent solutions are always obtainable are the cytotype frequencies in the two sexes, which at any time, $t = 0, 1, \ldots$, are

$$x_f^{(t)} = \bar{x}_f + (x_f^{(0)} - \bar{x}_f)(1 - m_f)^t \to \bar{x}_f. \text{ as } t \to \infty \quad (22)$$

and

$$x_m^{(t)} = m_m\bar{x}_m + (1 - m_m)\bar{x}_f + (1 - m_m)(x_f^{(0)} - \bar{x}_f)(1 - m_f)^{(t-1)} \to m_m\bar{x}_m + (1 - m_m)\bar{x}_f \text{ as } t \to \infty. \quad (23)$$

For females, the cytoplasmic frequency in the hybrid zone thus monotonically approaches the frequency in the migrant females ($\bar{x}_f$) at the constant rate of $1 - m_f$ per generation, while the cytotype frequency in males approaches a weighted average of the frequency in the migrant males and females, weighted by the total male migration rate, m_m. The equilibrium cytotype frequencies will be the same in both sexes only if there is no male migration ($m_m = 0$) or the cytotype frequencies in the male and female migrants are equal ($\bar{x}_f = \bar{x}_m$).

The equilibrium nuclear allele frequencies in the sexes are much more complex and are given by

$$\hat{p}_f = \frac{2m_f\bar{p}_f + (1 - m_f) \times [m_m\bar{p}_m(1 - \alpha\hat{u}_{1s} - \beta\hat{w}_{2s}) + \alpha\hat{u}_{1s}]}{2m_f + (1 - m_f) \times [m_m + (1 - m_m)(\alpha\hat{u}_{1s} + \beta\hat{w}_{2s})]} \quad (24)$$

and

$$\hat{p}_m = \frac{\begin{array}{l} m_m(1 + m_f)\bar{p}_m + (1 - m_m) \\ \times [2m_f\bar{p}_f + (1 - m_f)\alpha\hat{u}_{1s}] \end{array}}{\begin{array}{l} 2m_f + (1 - m_f) \\ \times [m_m + (1 - m_m)(\alpha\hat{u}_{1s} + \beta\hat{w}_{2s})] \end{array}}. \quad (25)$$

Due to the effects of assortative mating in the resident population, these values are not simple weighted averages of the migrant values, $\bar{p}_f$ and $\bar{p}_m$. Also, it should be emphasized that the final nuclear allele frequencies will usually not be equal in the two sexes, except in special cases such as when there is migration from only one sex ($m_m = 0$ or $m_f = 0$).

The equilibrium for the female allelic association, $\hat{D}_f$, can now be found by inserting (22), (24), (25), and $\hat{u}_{1s}$ and $\hat{w}_{2s}$ from APPENDIX B into (19d) and solving for the steady state, giving

$$\hat{D}_f = \frac{2m_f\bar{D}_f + (1 - m_f)(\alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f)}{1 + m_f}. \quad (26)$$

The female genotypic associations at equilibrium are similarly obtained from (19a)–(19c) as

$$\begin{aligned} \hat{D}_1 &= m_f\bar{D}_1 + (1 - m_f)(\hat{p}_m\hat{D}_f + \alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f) \\ \hat{D}_2 &= m_f\bar{D}_2 + (1 - m_f) \\ &\quad \times [(\hat{q}_m - \hat{p}_m)\hat{D}_f - \alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f] \\ \hat{D}_3 &= m_f\bar{D}_3 - (1 - m_f)(\hat{q}_m\hat{D}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f). \end{aligned}$$

In males, we find from (21), (22), (24), and (26) that the equilibrium allelic disequilibrium is

$$\begin{aligned} \hat{D}_m = m_m\bar{D}_m + (1 - m_m)\hat{D}_f \\ + m_m(1 - m_m)(\hat{p}_f - \bar{p}_m)(\bar{x}_f - \bar{x}_m), \end{aligned} \quad (27)$$

which will be a weighted average of the allelic disequilibrium in migrant males and the equilibrium allelic association in resident females if the migrant cytotype frequencies are the same for both sexes ($\bar{x}_f = \bar{x}_m$) or the equilibrium nuclear allele frequency in females is equal to the nuclear allele frequency in migrant males ($\hat{p}_f = \bar{p}_m$). The equilibria for the remaining variables are found by substituting the appropriate equilibrium values given above into the recursions in (16), (17) and (20).

There are four notable points regarding the steady-state values of the cytonuclear disequilibria within the hybrid zone. First, any female migration will generate permanent cytonuclear disequilibria in both sexes if there are nonrandom associations in the female migrants, as there are when the source populations are genetically differentiated at their nuclear and cytoplasmic loci. Male migration, however, can only generate permanent nonrandom associations in males. Second, paralleling the standard diploid model (ASMUSSEN *et al.* 1989), if the source populations are fixed for alternate nuclear and cytoplasmic alleles, the final female disequilibria satisfy $\hat{D}_3 < 0 < \hat{D}_1$, $\hat{D}_f$ with the sign of $\hat{D}_2$ being variable and depending on the mating and migration parameters. Moreover, at equilibrium, the female allelic disequilibrium in the hybrid zone must be less than the corresponding values in the migrant females (*i.e.*, $0 < \hat{D}_f < \bar{D}_f$) since, with diagnostic markers, $\hat{u}_{1s} < \bar{u}_{1s} = \bar{x}_f$ and $\hat{w}_{2s} < \bar{w}_{2s} = \bar{y}_f$ and hence, in the numerator of (26), $\alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f < \bar{x}_f\bar{y}_f(\hat{p}_m + \hat{q}_m) = \bar{D}_f$. Finally, due to the close dependence of males upon females, the sign of $\hat{D}_m$ is variable even when the source populations are fixed for alternate alleles, and there is no simple relationship between the magnitudes of the corresponding male disequilibria, $\hat{D}_m$ and $\bar{D}_m$.

Special case of random mating: If all individuals in the hybrid zone mate at random ($\alpha = \beta = 0$), several additional details of the cytonuclear system may be discerned. For example, in addition to the time-dependent solutions for the cytotype frequencies given in (22) and (23), it is possible to obtain the dynamical solutions for $p_f^{(t)}$, $p_m^{(t)}$, and $D_f^{(t)}$ (APPENDIX C), which fully determine the cytonuclear dynamics for all but the frequencies of the pure species individuals. The equilibria for the nuclear allele frequencies are now simply weighted averages of the frequencies in the migrant males and females ($\bar{p}_f$, $\bar{p}_m$), with

$$\begin{aligned} \hat{p}_f &= \frac{2m_f\bar{p}_f + (1 - m_f)m_m\bar{p}_m}{2m_f + (1 - m_f)m_m} \\ \hat{p}_m &= \frac{2m_f(1 - m_m)\bar{p}_f + (1 + m_f)m_m\bar{p}_m}{2m_f(1 - m_m) + (1 + m_f)m_m}. \end{aligned} \quad (28)$$

Thus, in random mating zones, the nuclear allele frequency will equilibrate in the two sexes if and only if $\bar{p}_f = \bar{p}_m = \bar{p}$, in which case the values in both sexes converge to the common migrant value ($\hat{p}_f = \hat{p}_m = \bar{p}$). In general, the asymptotic rate of approach to equilibrium by the nuclear alleles will be either faster than, equal to, or slower than the constant geometric rate, $1 - m_f$, for the cytotypes depending on whether the female migration rate (m_f) is less than, equal to, or greater than the male migration rate (m_m).

In random mating hybrid zones, the final female disequilibria are also simplified due to the equilibrium female allelic association reducing to

$$\hat{D}_f = \frac{2m_f\bar{D}_f}{1 + m_f},$$

which is approached at the asymptotic rate of $1 - m_f$ per generation. The equilibrium allelic association in males ($\hat{D}_m$) in (27) also simplifies due to the fact that

$$\hat{p}_f - \bar{p}_m = \frac{2m_f(\bar{p}_f - \bar{p}_m)}{2m_f + (1 - m_f)m_m}$$

is now just a constant multiple of $\bar{p}_f - \bar{p}_m$. Consequently, within random mating zones, there is an admixture effect upon $\hat{D}_m$ only if the migrant nuclear and cytotype

frequencies both differ between the sexes ($\bar{p}_f \neq \bar{p}_m$ and $\bar{x}_f \neq \bar{x}_m$).

Special cases of migration: In this section, we explore the distinctive features of five important special cases of migration that are subsumed under the general continent-island framework discussed above.

No migration ($m_f = m_m = 0$): Such a situation may occur if an established hybrid zone becomes disconnected from its source population(s). This results in a significantly different cytonuclear structure, because the dynamics reflect the effects of mating alone. For instance, the cytonuclear equilibrium is not unique and will depend upon both the assortative mating parameters and the initial genotype frequencies. Another general feature of a closed population is that the cytotype frequency in females remains at its initial value, and after the first generation of mating, the cytotype frequency in males will also take on and retain the initial value in females (*i.e.*, $x_f^{(t)} \equiv x_m^{(t)} \equiv x_f^{(0)}$ for $t \geq 1$).

The two remaining distinctions of this case stem specifically from the absence of migration by pure parentals and males. On the one hand, the lack of input of pure parentals means that their frequencies will decay to zero provided that assortative mating is incomplete ($0 \leq \alpha, \beta < 1$). This has important consequences since, in the absence of pure females, all individuals will mate at random, and the cytonuclear variables will be governed by the basic Hardy-Weinberg dynamics in (4)–(9). Once this happens, the cytonuclear disequilibria in both sexes will rapidly decay to zero. The lack of male gene flow, on the other hand, means that all male cytonuclear values will always lag one generation behind those in the females. Ultimately, the male values will equal those in females, but the common equilibrium nuclear allele frequency in males and females will not necessarily be the overall initial value, $p = \frac{2}{3}p_f^{(0)} + \frac{1}{3}p_m^{(0)}$, expected in a closed random mating population since assortative mating by the pure species females may alter the nuclear allele frequencies in the early generations.

Migration from only one population ($0 < m_f^{(1)}, m_m^{(1)} < 1$; $m_f^{(2)} = m_m^{(2)} = 0$): This is the standard continent-island formulation whereby migrants arrive from a single source (HARTL and CLARK 1989). If the migrants are of arbitrary composition, then the cytonuclear variables in the hybrid zone behave according to the general case with arbitrary values in the migrant pool. The more interesting situation occurs when the single source population is fixed at the nuclear and cytoplasmic loci. In this case, the resident population will become fixed for the same alleles and consequently all disequilibria will ultimately decay to zero. Surprisingly, even though the "hybrid zone" becomes monomorphic for both markers, it may not consist only of true pure parentals. Although fixation for the incoming pure types is a valid equilibrium state, it is unstable (see APPENDIXES A and B) if

$$\alpha < 1 - \frac{m_f}{(1 - m_f)(1 - m_m)} \quad \text{and} \quad m_f < \frac{1 - m_m}{2 - m_m} < \tfrac{1}{2}.$$

Under these conditions, there is a locally stable equilibrium at which the frequency of pure individuals within the hybrid zone are

$$\hat{u}_{1s} = \frac{m_f}{(1 - \alpha)(1 - m_f)(1 - m_m)} < 1$$

and

$$\hat{p}_{1s}^{m} = \frac{m_f + (1 - \alpha)(1 - m_f)m_m}{(1 - \alpha)(1 - m_f)} < 1$$

with $\hat{u}_{2s} = \hat{q}_{2s}^{m} = 0$. Therefore, the final composition of the hybrid zone will be a mixture of the incoming pure type individuals and pseudo-pure types with hybrid ancestry, if the total female migration rate is sufficiently below 0.5 and the assortative mating rate by the incoming pure type females is below a threshold level determined by the total male and female migration rates. This result reflects the fine, genealogical distinctions made by the model, and it is somewhat paradoxical since the "hybrid" individuals in the equilibrium hybrid zone would be fixed for species 1 alleles at all loci, and therefore would be genetically indistinguishable from the pure type individuals.

Male migration only ($m_f = 0$, $0 < m_m < 1$): If only males migrate into the hybrid zone and assortative mating is incomplete ($0 \leq \alpha, \beta < 1$), then the frequencies of both pure type females will decrease to zero. However, pure type males of species 1 and 2 will persist in the hybrid zone (provided that $0 < \bar{p}_{1s}^{m}, \bar{q}_{2s}^{m} < 1$) at frequencies of $m_m\bar{p}_{1s}^{m}$ and $m_m\bar{q}_{2s}^{m}$, respectively, that equal the products of the total male migration rate and the pure species frequencies in male migrants. Without female migration, the cytotype frequency in females will remain at its initial value (*i.e.*, $x_f^{(t)} \equiv x_f^{(0)}$ for all $t \geq 0$), and the cytoplasmic frequency in males will immediately stabilize at

$$\hat{x}_m = m_m\bar{x}_m + (1 - m_m)x_f^{(0)},$$

which is a weighted average of the value in migrant males and the initial value in the resident females. In contrast to the cytotype frequencies, the nuclear allele frequencies in both sexes are dominated by the male migration, with both approaching the frequency in the male migrants ($\bar{p}_m$). The final distinctive feature of this case is that, in the absence of female migration, all female disequilibria must ultimately decay to zero, but permanent male allelic disequilibrium will be present in the hybrid zone at a level of $\hat{D}_m = m_m\bar{D}_m$, provided that there are nonrandom allelic associations in the male migrants (as there are if migrants are derived from two genetically distinct source populations).

Female migration only ($0 < m_f < 1$, $m_m = 0$): When males do not migrate into the hybrid zone, all male

cytonuclear variables will always equal the analogous female values in the previous generation (*e.g.*, $p_m^{(t)} = p_f^{(t-1)}$), and therefore each male equilibrium will equal its counterpart in females (*e.g.*, $\hat{p}_{1s}^m = \hat{u}_{1s}$, $\hat{D}_m = \hat{D}_f$, $\hat{x}_m = \hat{x}_f = \bar{x}_f$). Moreover, in contrast to the case of male migration only, the continued input of pure parental females ensures that both pure females and males will persist in the hybrid zone, since pure females produce pure males parthenogenetically.

Equal migration rates of the sexes ($m_f^{(1)} = m_m^{(1)} = m^{(1)}$ and $m_f^{(2)} = m_m^{(2)} = m^{(2)}$: The only real simplification comes when the cytonuclear frequencies are the same in the male and female migrants (*e.g.*, $\bar{u}_{1s} = \bar{p}_{1s}^m$, $\bar{p}_f = \bar{p}_m$, $\bar{p}_1^f = \bar{p}_1^m$), as occurs if the two source populations are fixed for alternate alleles. In this case, the cytotype frequencies in both sexes equilibrate after the first generation ($x_m^{(t)} \equiv x_f^{(t)}$ for all $t \geq 1$) and monotonically approach the migrant cytotype frequency ($\bar{x} = \bar{x}_f = \bar{x}_m$). The final male disequilibrium is $\hat{D}_m = m\bar{D} + (1 - m)\hat{D}_f$, which is a simple weighted average of the allelic disequilibrium in the migrants ($\bar{D} = \bar{D}_f = \bar{D}_m$) and the final allelic association in females, weighted by the total migration rate in each sex ($m = m_f = m_m$).

Effect of census time: Under the alternative census scheme developed in APPENDIX D, the hybrid zone is censused after mating but before migration (census 2, see Figure 2). The most significant similarity and difference between the two censuses both concern the cytoplasmic marker. The important parallel is that the only variable whose equilibrium and dynamics are the same under both census schemes is the female cytoplasmic frequency (x_f), which, in both cases, converges monotonically to the value in the migrant females ($\bar{x}_f$) at the constant rate of $1 - m_f$ per generation. The major contrast is that, under census 2, the cytotype frequency in males will equal that in females after one generation, while under census 1 the two sexes have distinctive cytoplasmic frequency dynamics.

With the exception of the cytotype frequency in females, all frequency variables at each census after migration and before mating (z_1), and the previous census before migration and after mating (z_2) are simply related to one another by an equation of the form

$$z_1^{(t)} = m\bar{z} + (1 - m)z_2^{(t)} \tag{29}$$

for all $t \geq 1$, where $\bar{z}$ is the overall value of the variable in the sex-specific migrant pool. This equation holds for all female frequency variables with m replaced by m_f, and for all male frequency variables with m_m substituted for m. At equilibrium, the same relationship,

$$\hat{z}_1 = m\bar{z} + (1 - m)\hat{z}_2, \tag{30}$$

applies to all variables but the male allelic disequilibrium ($\hat{D}_m$). The relationship between the latter under the two census schemes is less simple and is given by

$$\hat{D}_{m(1)} = m_m\bar{D}_m + (1 - m_m)\hat{D}_{m(2)} + m_m(1 - m_m)(\hat{p}_{m(2)} - \bar{p}_m)(\bar{x}_f - \bar{x}_m), \tag{31}$$

where the parenthetical subscripts denote census times.

An even stronger connection exists between the sexes across the two census times. Since mating and reproduction separate each census 1 from the subsequent census 2 (Figure 2), and males receive all their alleles from their mothers, each male variable under census 2 will always equal the corresponding female variable at the prior census 1 (*i.e.*, $z_{m(2)}^{(t)} \equiv z_{f(1)}^{(t)}$). Thus, all male equilibria under census 2 will equal their female counterparts under census 1 ($\hat{z}_{m(2)} = \hat{z}_{f(1)}$). Looked at another way, with the exception of the cytotype frequency, which is always the same in both sexes immediately after mating, the male values under census 2 are half a generation behind those in females.

Inspection of (30) reveals several other important details concerning the equilibrium values at the different census times (with the exception of $\hat{x}_f$, $\hat{x}_m$, and $\hat{D}_m$). For example, as in the standard diploid model (ASMUSSEN *et al.* 1989) only three relationships are possible when comparing a value in the migrants, $\bar{z}$, and the corresponding equilibria under census 1 ($\hat{z}_1$) and census 2 ($\hat{z}_2$): $\hat{z}_2 < \hat{z}_1 < \bar{z}$, $\bar{z} < \hat{z}_1 < \hat{z}_2$, or $\hat{z}_1 = \hat{z}_2 = \bar{z}$ The equilibrium values under census 1 will therefore always be closer to the values in the migrants than those under census 2, and, since the frequency of pure parental females in the hybrid zone must be less than that in the migrant pool (see APPENDIX B), censusing directly after migration (census 1) will reveal a greater frequency of pure females. (This relationship is not necessarily true for males since the equilibrium frequency of pure type males can be greater than their frequency in migrants as shown in APPENDIX B). Similar reasoning shows that when the sources are fixed for alternate alleles, the final allelic disequilibrium in females will also be greater under census 1, since the equilibrium female allelic association in the residents is then necessarily less than that in the female migrants ($\hat{D}_f < \bar{D}_f$); the relationships for the other disequilibria are not as simple and depend on the migration rates and assortative mating parameters.

CONTINENT ISLAND MODELS FOR *X*-LINKED LOCI

Due to the differing modes of male production, the *X*-linked recursions for the pure species males differ from those for haplodiploids. Considering first the case of census 1, the *X*-linked analogues of (20) are as follows:

$$(p_{1s}^m)' = m_m\bar{p}_{1s}^m + (1 - m_m)u_{1s}[\alpha + (1 - \alpha)p_{1s}^m]$$
$$(q_{2s}^m)' = m_m\bar{q}_{2s}^m + (1 - m_m)w_{2s}[\beta + (1 - \beta)q_{2s}^m]. \tag{32}$$

These are the only variables whose recursions differ between the two systems, however, this difference gen-

erally affects the dynamics of the pure species females and affects the time-dependent values of all variables except the two cytotype frequencies if the pure species individuals mate assortatively ($\alpha \neq 0$ or $\beta \neq 0$). Turning to the steady state of the *X*-linked system, we find that a unique, locally stable equilibrium exists with $0 < \hat{u}_{1s}$, $\hat{w}_{2s}$, $\hat{p}^m_{1s}$, $\hat{q}^m_{2s} < 1$ if $0 < m_f$, $\bar{u}_{1s}$, $\bar{w}_{2s} < 1$ and $0 \leq \alpha$, β, m_m, $\bar{p}^m_{1s}$, $\bar{q}^m_{2s} < 1$ (see APPENDIX E). Although the equilibria of both pure females and males (presented in APPENDIX E) differ from the haplodiploid model, the qualitative relationships to their corresponding frequencies in the migrant pool are still satisfied (*i.e.*, $\hat{u}_{1s} < \bar{u}_{1s}$ and $\hat{w}_{2s} < \bar{w}_{2s}$, but $\hat{p}^m_{1s}$ and $\hat{q}^m_{2s}$ not necessarily less than $\bar{p}^m_{1s}$ and $\bar{q}^m_{2s}$, respectively). The equilibrium formulas for all other variables take on the same forms as in the haplodiploid model, but (with the exception of the cytotype frequencies) the actual final values differ due to their dependence on the equilibrium frequencies of the pure parentals if there is assortative mating.

A numerical analysis conducted by choosing values of m_f, m_m, $\bar{p}^m_{1s}$, $\bar{q}^m_{2s}$, $\bar{u}_{1s}$, $\bar{w}_{2s}$, α, and β from a grid on (0,1) of mesh 0.01 revealed that, at equilibrium, the frequencies of the pure parental males and females will both be greater under the haplodiploid model than under the *X*-linked model given the same parameter values. This result makes intuitive sense if we consider that the production of pure type males requires mating under the *X*-linked, diploid framework, but not under the haplodiploid system. Thus, under the haplodiploid model, the method of male production leads to a higher frequency of pure type males, whose presence concomitantly leads to a higher frequency of pure type females.

Special cases: There are no qualitative differences at census 1 in the behavior of the cytonuclear variables under the *X*-linked and haplodiploid models when the pure species mate at random ($\alpha = \beta = 0$), but four of the special cases of migration discussed above do lead to important differences in the dynamical and equilibrium frequencies of the pure parental species.

No migration ($m_f = m_m = 0$): For this case, the distinctive feature of the *X*-linked system is that the frequency of the pure parental males will equal the frequency of pure parental females after the first generation of mating (*i.e.*, $p^{m(t)}_{1s} \equiv u^{(t)}_{1s}$ and $q^{m(t)}_{2s} \equiv w^{(t)}_{2s}$ for all $t \geq 1$).

Migration from only one population ($0 < m_f^{(1)}$, $m_m^{(1)} < 1$; $m_f^{(2)} = m_m^{(2)} = 0$): If the single source population is fixed at the nuclear and cytoplasmic loci, we again have the seeming paradox that the population will not necessarily consist of truly pure parental types at equilibrium. For the *X*-linked system, fixation for the pure parental types ($\hat{u}_{1s} = \hat{p}^m_{1s} = 1$) is unstable (see APPENDIX E) if $m_f < 1 - m_m$ and

$$\alpha < \frac{1 - m_f - m_m}{1 - m_m},$$

and the frequencies of pure individuals within the hybrid zone then have the stable, steady-state values of

$$\hat{u}_{1s} = \frac{m_f}{(1 - \alpha)(1 - m_m)} < 1$$

and

$$\hat{p}^m_{1s} = \frac{\alpha m_f + (1 - \alpha) m_m}{(1 - \alpha)(1 - m_f)} < 1$$

with $\hat{w}_{2s} = \hat{p}^m_{2s} = 0$.

Female migration only ($0 < m_f < 1$, $m_m = 0$): In this case, our simple model breaks down in that it leads to the conclusion that both pure type males and females will be maintained within the hybrid zone at nonzero frequencies as long as there is continued input of pure females and they do not mate at random (α, $\beta > 0$). This result stems from the implicit assumption of our mating model that a female that chooses to mate assortatively will necessarily be able to do so. Realistically, however, without male migration, pure parental males should ultimately be eliminated from the hybrid zone after which no further conspecific matings can occur and no further pure type males can be produced.

Equal migration rates of the sexes ($m_f^{(1)} = m_m^{(1)} = m^{(1)}$ and $m_f^{(2)} = m_m^{(2)} = m^{(2)}$): If the corresponding frequencies are equal in the female and male migrants, as they are when populations are fixed for alternate alleles, then the pure parentals of both sexes will be found at equal frequencies after the first generation (*i.e.*, $u^{(t)}_{1s} \equiv p^{m(t)}_{1s}$ and $w^{(t)}_{2s} \equiv q^{m(t)}_{2s}$ for $t \geq 1$), as in the case of no migration.

Effect of census time: When censusing occurs after mating, the *X*-linked recursions for the pure types change to

$$u'_{1s} = (p^m_{1s})' = \tilde{u}_{1s}[\alpha + (1 - \alpha)\tilde{p}^m_{1s}]$$

$$w'_{2s} = (q^m_{2s})' = \tilde{w}_{2s}[\beta + (1 - \beta)\tilde{q}^m_{2s}], \qquad (33)$$

where $\tilde{z} = m\bar{z} + (1 - m)z$ with m replaced by m_f for $z = u_{1s}$ and w_{2s}, and m replaced by m_m for $z = p^m_{1s}$ and q^m_{2s}. Thus, the distinctive feature of this census for the *X*-linked system is that the dynamical and equilibrium frequencies of the pure parental females and males are identical (*i.e.*, $u^{(t)}_{1s} \equiv p^{m(t)}_{1s}$ and $w^{(t)}_{2s} \equiv q^{m(t)}_{2s}$ for $t \geq 1$). The final frequencies of the parental species under census 2 can be obtained from the relationship between the censuses given in (30) and the equilibria for census 1 given in APPENDIX E. The sexual mode of male production in the *X*-linked diploid model also means that the general intercensus relationship for the haplodiploid model, in which male variables under census 2 equal the corresponding female variables under census 1, breaks down for the pure species males. The only special case with additional intercensus differences for the pure species is that of male migration only ($m_f = 0$, $0 < m_m < 1$), for which no pure individuals of either sex are maintained under census 2, but pure males are present at equilibrium under census 1.

DISCUSSION

We have developed the first theoretical frameworks necessary to analyze the cytonuclear structure for haplodiploid species or *X*-linked genes in diploid species. Due to the ploidy differences between the sexes, the basic cytonuclear frequencies and disequilibria in such systems require new, sex-specific definitions. The cytonuclear structure of the diploid females is analogous to that in the standard, diploid case (ASMUSSEN *et al.* 1987) in that for diallelic markers there are six joint genotypes, with one allelic and three genotypic disequilibria. Consequently, estimates and significance of the cytonuclear disequilibria in females can be calculated from population samples by following existing procedures for the standard, diploid formulation (ASMUSSEN *et al.* 1987; ASMUSSEN and BASTEN 1994, 1996; DEAN and ARNOLD 1996; BASTEN and ASMUSSEN 1997). The genetic architecture of haploid males, however, deviates from the standard, cytonuclear framework in that for diallelic markers there are only four joint genotypes and only a single, allelic disequilibrium. Because the structure of the male data parallels that of gametic data from purely nuclear systems, estimates and significance of male disequilibria can be obtained via established methods for analyzing two-locus gametic phase disequilibrium from nuclear haplotype data (WEIR 1996).

As a first step toward understanding and interpreting observed cytonuclear associations in haplodiploid and *X*-linked systems, we analyzed the dynamical behavior of their disequilibria under Hardy-Weinberg conditions. A major finding is that the male allelic disequilibrium (D_m) lags one generation behind, and takes on twice the value of, the allelic disequilibrium in females (D_f) after the first generation of random mating. Furthermore, D_m, and the female homozygote disequilibrium, D_1, immediately take on and retain the initial sign of D_f, while the alternate female homozygote disequilibrium, D_3, takes on the opposite sign. This sign pattern parallels that found in the standard diploid model (ASMUSSEN *et al.* 1987), except here the signs depend solely on the initial female allelic disequilibrium. Although all cytonuclear disequilibria rapidly decay to zero under Hardy-Weinberg conditions, the ploidy differences between the sexes allow interesting nonmonotonic behavior in the initial generations.

Our primary focus has been on determining the effects of hybridization on cytonuclear structure for haplodiploid species or for *X*-linked genes in diploid species. We began by deriving the precise effects of population admixture on the cytonuclear disequilibria, which revealed that differences in both the nuclear and cytoplasmic frequencies in the same sex can lead to an admixture effect, in which the sex-specific disequilibrium in the combined population differs from the average association found in its components. We then expanded the admixture framework by developing and analyzing continent-island models of hybridization, whereby individuals from two genetically differentiated source populations migrate into and mate in a single hybrid zone. Our models allow for differential migration of the sexes and assortative mating, and they take into account the timing of the census [*i.e.*, after migration and before mating (census 1) or before migration and after mating (census 2)]. Analysis of the equilibrium structure of these models reveals that, when the nuclear and cytoplasmic loci are diagnostic for the two source populations, pure parental individuals and cytonuclear disequilibria will be maintained in hybrid zones provided there is continued migration of both sexes from the two source populations. The genetic importance of the females, who are diploid at their nuclear locus and solely responsible for the transmission of the cytoplasmic marker, is evidenced by the fact that, under both census times, female migration alone ensures that there will be permanent cytonuclear disequilibrium in both sexes, while migration solely by males maintains permanent disequilibrium in males only and only under census 1.

Although the two censuses generally concur in the presence or absence of nonrandom associations, the magnitude of the cytonuclear disequilibria can vary substantially with the census time, and it is therefore important to know when censusing has occurred relative to mating and migration in order to correctly interpret cytonuclear disequilibria within a hybrid zone. In general, since mating tends to break up nonrandom genetic associations, the cytonuclear associations are apt to be greater in magnitude, and therefore more likely to be detected, immediately after migration (census 1) than immediately after mating (census 2). Another important point related to the timing of the census is that [with the single exception of the frequency of pure males under the *X*-linked model (see below)], in every generation, the value of any male variable under census 2 will always equal the corresponding female variable under census 1. This result follows directly from the fact that, in haplodiploid and *X*-linked systems, both the cytoplasmic and nuclear complement of males are derived exclusively from their mothers. Finally, it is worth noting that the only variable whose behavior is the same under both censuses is the female cytotype frequency. This observation, coupled with the previously mentioned intercensus relationship between male and female variables, leads to the key intercensus difference that, at any time, the cytotype frequencies will be the same in both sexes under census 2, but will usually differ under census 1.

In general, the cytonuclear disequilibria within a natural hybrid zone should be easiest to interpret when the two source populations are fixed for alternate alleles, because the expected patterns of the associations are then particularly straightforward. In females, the equilibrium sign pattern parallels that found in the stan-

dard, diploid system (ASMUSSEN *et al.* 1989) in that under either census, the female allelic disequilibrium, $\hat{D}_f$, and the homozygote disequilibrium, $\hat{D}_1$, will both be positive, while the alternate homozygote disequilibrium, $\hat{D}_3$, is negative; the sign of the heterozygote disequilibrium, $\hat{D}_2$, is variable and depends on the migration and assortative mating parameters. Also, with fixed differences between the sources, the female allelic association in the hybrid zone must always be less than that in the migrants ($0 < \hat{D}_f < \bar{D}_f$). In contrast to the disequilibrium patterns found in the females, only under census 2 are we ensured that the sign of the single, male allelic disequilibrium ($\hat{D}_m$) will be positive with diagnostic markers. Furthermore, there is no simple relationship between the male disequilibrium in the hybrid zone and that in the male migrants.

Examination of important special cases of migration has revealed several additional points. For example, in situations where migration from one source population is curtailed, the "hybrid zone" may not necessarily become fixed for the pure species arriving from the single source population, even though all individuals will become fixed for its alleles at all loci. The reason for this apparent paradox is that some of the resident individuals are distantly derived from hybrids so they are not considered pure by the strict definition, although they would be indistinguishable from pure type individuals genetically. Furthermore, results from some of the special cases may be useful in detecting patterns of migration in hybrid zones. Migration of only males can be detected by examination of the frequency of pure parental types and male disequilibrium under both census times; pure males and male disequilibrium should be maintained under census 1, but not under census 2. On the other hand, if only female migration occurs, then the equilibrium frequency of the nuclear alleles will be the same in the two sexes under census 1, but will usually differ under census 2.

Another discovery of considerable practical importance is that separate models are needed to analyze hybrid zone data from haplodiploids and *X*-linked systems when pure type individuals are distinguished. This dichotomy results from the fact that males are produced parthenogenetically in haplodiploid species whereas they are produced sexually in diploid species, thereby yielding distinct dynamics for the pure species males. Although the recursions and qualitative behavior for all of the other variables in the *X*-linked system are identical to those for haplodiploids, the frequency of the pure parental females will generally be different as will the actual values of all of the variables (except the cytotype frequencies) if either of the pure parental females mates assortatively. One important result stemming from the distinction between the *X*-linked and haplodiploid models is that the equilibrium frequency of pure parental males and females will both be higher under the haplodiploid model for identical parameter values. Another noteworthy difference is that, under the *X*-linked formulation only, the frequencies of the pure parental males and females will be identical when censusing after mating but before migration (census 2), but usually differ when censusing directly after migration (census 1). For the haplodiploid model, the frequencies of the pure parentals are not expected to be the same under either census except in certain special cases, such as that of female migration only and only under census 1.

The models that we have developed can be used to estimate sex-specific rates of migration and assortative mating by pure parentals within a hybrid zone by extending the maximum likelihood methods developed for the standard, diploid formulation (ASMUSSEN *et al.* 1989). We wished to assess these values in an area of hybridization between two haplodiploid ant species, *Solenopsis invicta* and *S. richteri*. These two pests were introduced earlier this century, and they now form a large hybrid zone that spans across much of northern Alabama, Mississippi, and Georgia (VINSON and GREENBERG 1986). However, the size of the hybrid zone, (*ca.* 70 km), is considerably larger than the migration rate of a fire ant queen (1–10 km) (MARKIN *et al.* 1972). Therefore, use of the continent-island model we have developed, which assumes that the hybrid zone consists of a single area of mating and reproduction, would be inappropriate. This has motivated us to expand our models to incorporate the effects of population structure within hybrid zones in which migration is restricted to adjacent subpopulations. This important subject will be treated elsewhere.

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APPENDIX A
LOCAL STABILITY ANALYSIS FOR HAPLODIPLOID MODEL UNDER CENSUS 1

The cytonuclear recursions for census 1 depend on only eight variables: u_{1s}, p^m_{1s}, w_{2s}, q^m_{2s}, p_f, p_m, D_f, and x_f. Therefore, the equilibrium for the entire system will be locally stable if the eight local stability eigenvalues associated with these eight basic variables are all less than one in magnitude. These eigenvalues satisfy the characteristic equation

$$\left(\frac{\partial x'_f}{\partial x_f} - \lambda\right)\left(\frac{\partial D'_f}{\partial D_f} - \lambda\right) f_1(\lambda) f_2(\lambda) f_3(\lambda) = 0, \quad \text{(A1)}$$

where

$$f_1(\lambda) = \lambda^2 - \frac{\partial u'_{1s}}{\partial u_{1s}}\lambda - \left(\frac{\partial u'_{1s}}{\partial p^m_{1s}}\right)\left(\frac{\partial (p^m_{1s})'}{\partial u_{1s}}\right) \quad \text{(A2)}$$

is the characteristic equation for the pure species 1 subsystem (u_{1s}, p^m_{1s}), $f_2(\lambda)$ and $f_3(\lambda)$ are the analogous characteristic equations for the pure species 2 (w_{2s}, q^m_{2s}) and the nuclear allele frequency (p_f, p_m) subsystems, and all partial derivatives are evaluated at the equilibrium. The first two eigenvalues,

$$\lambda_1 = \frac{\partial x'_f}{\partial x_f} = 1 - m_f \quad \text{and} \quad \lambda_2 = \frac{\partial D'_f}{\partial D_f} = \frac{1}{2}(1 - m_f),$$

will be less than one in magnitude provided that all females in the hybrid zone are not replaced each generation ($0 < m_f < 1$).

The three remaining factors of (A1) are all quadratics of the form $f_i(\lambda) = \lambda^2 - A_i\lambda + B_i$ with $A_i > 0$ and real roots (since in each case $A_i^2 - 4B_i > 0$). The roots of such equations lie in $(-1, 1)$, if and only if $A_i < 2$ and $A_i < 1 + B_i$ (GOLDBERG 1958). Expansion of the first quadratic shows that

$$A_1 = (1 - m_f)[\alpha + (1 - \alpha)\hat{p}^m_{1s}]$$

and

$$B_1 = -(1 - \alpha)(1 - m_f)(1 - m_m)\hat{u}_{1s}$$

with $\hat{p}^m_{1s}$ and $\hat{u}_{1s}$ given by (B2) and the smaller solution of (B1). Since $0 < A_1 < 1$, λ_3 and λ_4 lie in $(-1, 1)$, if

$$\hat{u}_{1s} < \frac{1 - (1 - m_f)[\alpha + (1 - \alpha) m_m \bar{p}^m_{1s}]}{2(1 - \alpha)(1 - m_f)(1 - m_m)}. \quad \text{(A3)}$$

The right-hand side of this inequality is the critical point and minimum of the quadratic defining $\hat{u}_{1s}$ given in (B1). Since $\hat{u}_{1s}$ is the smaller of the two roots of this quadratic, (A3) must hold whenever the equilibrium exists. Analogous arguments show that the eigenvalues, λ_5 and λ_6, obtained from the second quadratic factor, $f_2(\lambda)$, of (A1) always lie in $(-1, 1)$. The coefficients of the final factor, $f_3(\lambda)$, are

$$A_3 = \tfrac{1}{2}(1 - m_f)$$

and

$$B_3 = -\tfrac{1}{2}(1 - m_f)(1 - m_m)(1 - \alpha\hat{u}_{1s} - \beta\hat{w}_{2s}).$$

Since $0 < A_3 < \tfrac{1}{2}$, the final two eigenvalues, λ_7 and λ_8, will have magnitude less than one provided that

$$(1 - m_f)[1 + (1 - m_m)(1 - \alpha\hat{u}_{1s} - \beta\hat{w}_{2s})] < 2,$$

which always holds. Combining all these results with the existence conditions in APPENDIX B, we conclude that whenever $0 < m_f, \bar{u}_{1s}, \bar{w}_{2s} < 1$ and $0 \leq \alpha, \beta, m_m < 1$, a unique, nontrivial cytonuclear equilibrium will exist with $0 < \hat{u}_{1s}, \hat{w}_{2s}, \hat{p}^m_{1s}, \hat{q}^m_{2s} < 1$, and it will be locally stable.

APPENDIX B
EQUILIBRIUM FREQUENCIES OF HAPLODIPLOID PURE PARENTALS UNDER CENSUS 1

Inspection of the recursions for u_{1s} and p^m_{1s} given in (15) and (20) shows that at equilibrium $\hat{u}_{1s}$ must satisfy

$$f(u_{1s}) = A_1 u_{1s}^2 + B_1 u_{1s} + C_1 = 0, \quad \text{(B1)}$$

where

$$A_1 = (1 - \alpha)(1 - m_f)(1 - m_m)$$

$$B_1 = (1 - \alpha)(1 - m_f) m_m \bar{p}^m_{1s} + \alpha(1 - m_f) - 1$$

$$C_1 = m_f \bar{u}_{1s}$$

with the corresponding male equilibrium given by

$$\hat{p}_{1s}^{m} = m_m \bar{p}_{1s}^{m} + (1 - m_m)\,\hat{u}_{1s}. \qquad \text{(B2)}$$

When $0 < m_f, \bar{u}_{1s} < 1$ and $0 \leq \alpha, m_m < 1$, then $f(0) > 0$, $f(1) < 0$, and $f(u_{1s}) > 0$ as $u_{1s} \to \pm\infty$; thus, in this case there is always exactly one solution, $u_{1s} = \hat{u}_{1s}$, in the admissible range of $0 < u_{1s} < 1$, which is given by the smaller root of (B1). Furthermore, since

$$f(\bar{u}_{1s}) = -(1 - \alpha)(1 - m_f) \times [1 - m_m \bar{p}_{1s}^{m} - (1 - m_m)\,\bar{u}_{1s}]\,\bar{u}_{1s} < 0,$$

and, on $(0, 1)$, $f(u_{1s}) < 0$ if and only if $\hat{u}_{1s} < u_{1s} < 1$, then it must always be true that $\hat{u}_{1s} < \bar{u}_{1s}$. This relationship is not necessarily true for pure type males, for which $\hat{p}_{1s}^{m} > \bar{p}_{1s}^{m}$ if $\bar{p}_{1s}^{m} < \bar{u}_{1s}$ and

$$\alpha > 1 - \frac{m_f(\bar{u}_{1s} - \bar{p}_{1s}^{m})}{(1 - m_f)\,\bar{p}_{1s}^{m}(1 - \bar{p}_{1s}^{m})}.$$

Analogous formulas and results hold for the pure species 2 individuals with u_{1s} replaced by u_{2s}, $\bar{u}_{1s}$ by $\bar{u}_{2s}$, p_{1s}^{m} by q_{2s}^{m}, $\bar{p}_{1s}^{m}$ by $\bar{q}_{2s}^{m}$, and α by β.

APPENDIX C
TIME-DEPENDENT SOLUTIONS FOR HAPLODIPLOIDS UNDER CENSUS 1 AND RANDOM MATING

Solutions for $p_f^{(t)}$, $p_m^{(t)}$, and $D_f^{(t)}$ at any time t can be obtained in the special case of random mating populations. The nuclear allele frequency dynamics take the form of $\mathbf{p}_{t+1} = \mathbf{A}\mathbf{p}_t + \mathbf{b}$ where $\mathbf{p}_t = (p_f^{(t)}, p_m^{(t)})^T$, $\mathbf{b} = (m_f\bar{p}_f, m_m\bar{p}_m)^T$, and the coefficient matrix $\mathbf{A}$ is

$$\mathbf{A} = \begin{pmatrix} \tfrac{1}{2}(1 - m_f) & \tfrac{1}{2}(1 - m_f) \\ 1 - m_m & 0 \end{pmatrix}.$$

Iterating this matrix recursion yields the solution

$$\mathbf{p}_t = \mathbf{A}^t\mathbf{p}_0 + \left(\sum_{i=0}^{t-1} \mathbf{A}^i\right)\mathbf{b} \quad \text{for} \quad t = 1, 2, \ldots,$$

where $\mathbf{A}^0 = \mathbf{I}$ is the 2×2 identity matrix. Using the spectral decomposition of the matrix $\mathbf{A}$, this simplifies to

$$\mathbf{p}_t = \mathbf{P}\Lambda^t\mathbf{P}^{-1}\mathbf{p}_0 + \mathbf{P}\left(\sum_{i=0}^{t-1} \Lambda^i\right)\mathbf{P}^{-1}\mathbf{b}.$$

Here,

$$\Lambda^i = \begin{pmatrix} \lambda_1^i & 0 \\ 0 & \lambda_2^i \end{pmatrix},$$

where

$$\lambda_1, \lambda_2 = \frac{1 - m_f \mp \sqrt{(1 - m_f)(9 - m_f - 8m_m)}}{4} \qquad \text{(C1)}$$

are the two eigenvalues of the matrix $\mathbf{A}$,

$$\mathbf{P} = \begin{pmatrix} \dfrac{\lambda_1}{1 - m_m} & \dfrac{\lambda_2}{1 - m_m} \\ 1 & 1 \end{pmatrix}$$

and

$$\mathbf{P}^{-1} = \frac{1}{\lambda_1 - \lambda_2}\begin{pmatrix} 1 - m_m & -\lambda_2 \\ -(1 - m_m) & \lambda_1 \end{pmatrix},$$

where the columns of the matrix $\mathbf{P}$ are the right eigenvectors of the matrix $\mathbf{A}$ corresponding to λ_1 and λ_2. After considerable algebra, we find that in any generation $t = 1, 2, \ldots,$

$$p_f^{(t)} = \left(\frac{k_1\lambda_1}{1 - m_m}\right)\lambda_1^t + \left(\frac{k_2\lambda_2}{1 - m_m}\right)\lambda_2^t + \hat{p}_f$$

$$p_m^{(t)} = k_1\lambda_1^t + k_2\lambda_2^t + \hat{p}_m, \qquad \text{(C2)}$$

where $\hat{p}_f$ and $\hat{p}_m$ are the equilibrium nuclear allele frequencies given in (28),

$$k_i = \frac{(1 - m_m)\,p_f^{(0)} - \lambda_j p_m^{(0)}}{\lambda_i - \lambda_j} + \frac{\lambda_j m_m \bar{p}_m - m_f(1 - m_m)\,\bar{p}_f}{(\lambda_i - \lambda_j)(1 - \lambda_i)} \qquad \text{(C3)}$$

for $i \neq j = 1, 2$, and $p_f^{(0)}$ and $p_m^{(0)}$ are the initial nuclear allele frequencies in females and males. For both $p_f^{(t)}$ and $p_m^{(t)}$, the dominant factor is λ_2^t, corresponding to the larger of the two eigenvalues.

Under random mating, the female allelic disequilibrium recursion reduces to

$$D_f^{(t+1)} = \tfrac{1}{2}(1 - m_f)\,D_f^{(t)} + \tfrac{1}{2}m_f(1 - m_f) \times (p_f^{(t)} + p_m^{(t)} - 2\bar{p}_f)(x_f^{(t)} - \bar{x}_f) + m_f\bar{D}_f. \qquad \text{(C4)}$$

After substituting in the time-dependent solutions for the allele frequencies given in (22) and (C2), we find that (C4) has the form

$$D_f^{(t+1)} = aD_f^{(t)} + c_1 d_1^t + c_2 d_2^t + c_3 d_3^t + b, \qquad \text{(C5)}$$

where the geometric factors are $a = \tfrac{1}{2}(1 - m_f)$, $d_1 = \lambda_1(1 - m_f)$, $d_2 = \lambda_2(1 - m_f)$, and $d_3 = 1 - m_f$; the constant factors are $b = m_f\bar{D}_f$,

$$c_i = \frac{1}{2}k_i m_f(1 - m_f)\left(1 + \frac{\lambda_i}{1 - m_m}\right)(x_f^{(0)} - \bar{x}_f),$$

for $i = 1, 2$, and,

$$c_3 = \frac{m_f(1 - m_f)\,m_m(\bar{p}_m - \bar{p}_f)(x_f^{(0)} - \bar{x}_f)}{2m_f + (1 - m_f)\,m_m},$$

where λ_1 and λ_2 are the eigenvalues in (C1) and k_1 and k_2 are the coefficients in (C3). Iterating the D_f recursion shows that in any generation t,

$$D_f^{(t)} = \left(D_f^{(0)} - \sum_{i=1}^{3} \frac{c_i}{d_i - a} - \hat{D}_f \right) a^t + \sum_{i=1}^{3} \frac{c_i d_i^t}{d_i - a} + \hat{D}_f, \quad \text{(C6)}$$

provided that $\lambda_2 \neq 1/2$, while if $\lambda_2 = 1/2$, then

$$D_f^{(t)} = \left(D_f^{(0)} + \frac{tc_2}{a} - \frac{c_1}{d_1 - a} - \frac{c_3}{d_3 - a} - \hat{D}_f \right) a^t + \frac{c_1 d_1^t}{d_1 - a} + \frac{c_3 d_3^t}{d_3 - a} + \hat{D}_f. \quad \text{(C7)}$$

In both solutions, (C6) and (C7), the dominant term is $d_3^t = (1 - m_f)^t$ and

$$D_f^{(t)} \to \hat{D}_f = \frac{b}{1 - a} = \frac{2m_f \bar{D}_f}{1 + m_f} \text{ as } t \to \infty.$$

APPENDIX D
CENSUS 2 FOR HAPLODIPLOIDS: AFTER MATING AND BEFORE MIGRATION

Under this second census scheme, each generation begins with an influx of migrants, which is then followed by mating (Figure 2). For this model, it is convenient to first define and calculate the cytonuclear frequencies and the female allelic disequilibrium after migration, since the cytonuclear recursions depend directly on these interim values. For any frequency variable z, this intermediate value is given by $\tilde{z} = m\bar{z} + (1 - m)z$, where $\bar{z}$ is the corresponding value in the migrants and m is the corresponding sex-specific migration rate, while the interim value of D_f after migration is given by

$$\tilde{D}_f = m_f \bar{D}_f + (1 - m_f) D_f + m_f(1 - m_f)(p_f - \bar{p}_f)(x_f - \bar{x}_f).$$

Analysis of a mating table shows that the haplodiploid recursions for the frequencies of the pure species females are

$$u'_{1s} = \tilde{u}_{1s}[\alpha + (1 - \alpha)\tilde{p}^m_{1s}]$$
$$w'_{2s} = \tilde{w}_{2s}[\beta + (1 - \beta)\tilde{q}^m_{2s}],$$

while those for the composite female cytonuclear genotypes are

$$u'_1 = \tilde{p}_f \tilde{p}_m + \alpha \tilde{u}_{1s} \tilde{q}_m \qquad u'_2 = \tilde{p}^2_f \tilde{p}_m$$
$$v'_1 = \tilde{p}_f \tilde{q}_m + \tilde{q}_f \tilde{p}_m - \alpha \tilde{u}_{1s} \tilde{q}_m \qquad v'_2 = \tilde{p}^2_f \tilde{q}_m + \tilde{q}^2_f \tilde{p}_m - \beta \tilde{w}_{2s} \tilde{p}_m$$
$$w'_1 = \tilde{q}_f \tilde{q}_m \qquad w'_2 = \tilde{q}^2_f \tilde{q}_m + \beta \tilde{w}_{2s} \tilde{p}_m. \quad \text{(D1)}$$

From these, we find that the new marginal nuclear genotype frequencies in females are

$$u' = \tilde{p}_f \tilde{p}_m + \alpha \tilde{u}_{1s} \tilde{q}_m$$
$$v' = \tilde{p}_f \tilde{q}_m + \tilde{q}_f \tilde{p}_m - \alpha \tilde{u}_{1s} \tilde{q}_m - \beta \tilde{w}_{2s} \tilde{p}_m$$
$$w' = \tilde{q}_f \tilde{q}_m + \beta \tilde{w}_{2s} \tilde{p}_m, \quad \text{(D2)}$$

while the new allele frequencies in females are

$$p'_f = 1/2(\tilde{p}_f + \tilde{p}_m + \alpha \tilde{u}_{1s} \tilde{q}_m - \beta \tilde{w}_{2s} \tilde{p}_m)$$
$$x'_f = \tilde{x}_f. \quad \text{(D3)}$$

From the disequilibrium definitions given in (1) and (2) and the frequency recursions in (D1) – (D3), we find that after one generation the four female cytonuclear disequilibria become

$$D'_1 = \tilde{p}_m \tilde{D}_f + \alpha \tilde{u}_{1s} \tilde{q}_m \tilde{y}_f$$
$$D'_2 = (\tilde{q}_m - \tilde{p}_m)\tilde{D}_f - \alpha \tilde{u}_{1s} \tilde{q}_m \tilde{y}_f + \beta \tilde{w}_{2s} \tilde{p}_m \tilde{x}_f$$
$$D'_3 = -\tilde{q}_m \tilde{D}_f - \beta \tilde{w}_{2s} \tilde{p}_m \tilde{x}_f$$
$$D'_f = 1/2(\tilde{D}_f + \alpha \tilde{u}_{1s} \tilde{q}_m \tilde{y}_f + \beta \tilde{w}_{2s} \tilde{p}_m \tilde{x}_f).$$

Since males are produced asexually and censusing occurs after reproduction, the value of any male variable in the next generation simply equals the corresponding interim, postmigrational value in females. This yields the recursions,

$$(p^m_{1s})' = \tilde{u}_{1s} \quad (q^m_{2s})' = \tilde{w}_{2s}$$
$$(p^m_i)' = \tilde{p}^f_i \quad (\tilde{q}^m_i)' = \tilde{q}^f_i \quad \text{(D4)}$$

for $i = 1, 2$ for the genotype frequencies, and

$$p'_m = \tilde{p}_f \quad x'_m = \tilde{x}_f \quad D'_m = \tilde{D}_f \quad \text{(D5)}$$

for the allele frequencies and disequilibrium in males.

Because of the intimate connection between the two censuses, the existence and local stability of a single equilibrium for this census time can be inferred from the corresponding analysis of census 1 (APPENDIX A). The equilibrium frequencies of pure type individuals, $\hat{u}_{1s}$, $\hat{w}_{2s}$, $\hat{p}^m_{1s}$, and $\hat{q}^m_{2s}$, can be obtained directly from the census 1 values (APPENDIX B) and the intercensus relationship in (30). The time-dependent solution for the female cytotype frequency has the same form as that under census 1 in (22). Moreover, the male cytotype frequency now has this very same dynamic, since we see from (D3) and (D5) that under census 2, $x_m^{(t)} \equiv x_f^{(t)}$ for all $t \geq 1$. The equilibrium nuclear allele frequencies in the two sexes are

$$\hat{p}_f = \frac{m_f \bar{p}_f + [m_f(1 - m_m)\bar{p}_f + m_m \bar{p}_m] \times (1 - \alpha \hat{\tilde{u}}_{1s} - \beta \hat{\tilde{w}}_{2s}) + \alpha \hat{\tilde{u}}_{1s}}{2m_f + (1 - m_f) \times [m_m + (1 - m_m)(\alpha \hat{\tilde{u}}_{1s} + \beta \hat{\tilde{w}}_{2s})]}$$

and

$$\hat{p}_m = \frac{2m_f \bar{p}_f + (1 - m_f) \times [m_m \bar{p}_m (1 - \alpha \hat{\tilde{u}}_{1s} - \beta \hat{\tilde{w}}_{2s}) + \alpha \hat{\tilde{u}}_{1s}]}{2m_f + (1 - m_f) \times [m_m + (1 - m_m)(\alpha \hat{\tilde{u}}_{1s} + \beta \hat{\tilde{w}}_{2s})]},$$

and the final disequilibria are

$$\hat{D}_f = \frac{m_f\bar{D}_f + \alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f}{1 + m_f}$$

$$\hat{D}_1 = \hat{p}_m\hat{\bar{D}}_f + \alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f$$

$$\hat{D}_2 = (\hat{q}_m - \hat{p}_m)\hat{\bar{D}}_f - \alpha\hat{u}_{1s}\hat{q}_m\bar{y}_f + \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f$$

$$\hat{D}_3 = -\hat{q}_m\hat{\bar{D}}_f - \beta\hat{w}_{2s}\hat{p}_m\bar{x}_f$$

$$\hat{D}_m = \hat{\bar{D}}_f,$$

where, for any variable z on the right-hand side, including D_f, $\hat{z} = m\bar{z} + (1 - m)\hat{z}$, with m replaced by m_f for female variables or by m_m for male variables. Note that the equilibrium sign pattern $\hat{D}_3 < 0 < \hat{D}_1, \hat{D}_f, \hat{D}_m$ holds for census 2 whenever there is a positive allelic association in the migrant females ($\bar{D}_f > 0$). The equilibria for the remaining variables can be obtained by substituting the equilibrium values above into the appropriate recursions given in (D1), (D2), and (D4).

Special case of random mating: If there is no assortative mating ($\alpha = \beta = 0$), the time-dependent solutions for the variables $p_f^{(t)}$, $p_m^{(t)}$, and $D_f^{(t)}$ are obtainable using the solutions for census 1 found in APPENDIX C together with the intercensus relationship given in (29) for the frequencies and

$$D_{f(1)}^{(t)} = m_f\bar{D}_f + (1 - m_f)D_{f(2)}^{(t)} + m_f(1 - m_f)(p_{f(2)}^{(t)} - \bar{p}_f)(x_{f(2)}^{(t)} - \bar{x}_f)$$

for the female disequilibrium, where the numerical subscripts denote census time. The equilibrium nuclear allele frequencies reduce to

$$\hat{p}_f = \frac{m_f(2 - m_m)\bar{p}_f + m_m\bar{p}_m}{m_f(2 - m_m) + m_m}$$

and

$$\hat{p}_m = \frac{2m_f\bar{p}_f + (1 - m_f)m_m\bar{p}_m}{2m_f + (1 - m_f)m_m},$$

which, like census 1, are weighted averages of $\bar{p}_f$ and $\bar{p}_m$. The steady-state disequilibria also simplify considerably, and the final male allelic disequilibrium is now simply twice the value in females,

$$\hat{D}_m = 2\hat{D}_f = \frac{2m_f\bar{D}_f}{1 + m_f}$$

with $\hat{D}_f$ now at most half the value in the migrant females (*i.e.*, $\hat{D}_f \leq {}^1/_2\bar{D}_f$). Under census 2, the equilibrium sign pattern of $\hat{D}_m$ and $\hat{D}_1$ having the same sign, and $\hat{D}_3$ the opposite sign of $\hat{D}_f$, is true in general for random mating populations and does not require fixed differences between the two sources.

Special cases of migration: Only two of the special cases of migration show qualitative differences between the censuses, above and beyond the general census 2 property of the cytotype frequency being the same in the sexes.

Male migration only ($0 < m_m < 1$, $m_f = 0$): Under this scenario, census 2 differs from census 1 in four, major qualitative ways. First, with censusing after mating, all male variables are exactly one generation behind the corresponding female variables (*i.e.*, $z_m^{(t)} = z_f^{(t-1)}$) and thus all male equilibria equal those in females ($\hat{z}_m = \hat{z}_f$). Second, no pure type individuals of either sex will be maintained within the hybrid zone, because pure type females are eventually eliminated from the hybrid zone, and once this happens, no pure males will be found immediately after reproduction of what are ultimately only hybrid females. The other two qualitative distinctions of census 2 for male migration only are that the cytotype frequencies in both sexes will always equal the initial value in females ($x_m^{(t)} \equiv x_f^{(t)} \equiv x_f^{(0)}$ for all $t \geq 1$) and all cytonuclear disequilibria (including $\hat{D}_m$) will ultimately decay to zero.

Female migration only ($0 < m_f < 1$, $m_m = 0$): The distinctive feature of this case is that, unlike census 1 where male variables lagged a full generation behind those in females, under census 2 the male variables (except x_m) are half a generation behind those in females, and therefore the male equilibria will not necessarily equal the corresponding values in females.

APPENDIX E
FREQUENCY OF PURE PARENTALS AND LOCAL STABILITY ANALYSIS UNDER *X*-LINKED MODEL FOR CENSUS 1

From the recursions given in (15) and (32), it can be shown that $\hat{u}_{1s}$ must satisfy the quadratic equation

$$f(u_{1s}) = A_1u_{1s}^2 + B_1u_{1s} + C_1 = 0, \qquad \text{(E1)}$$

where

$$A_1 = (1 - \alpha)(1 - m_m)$$

$$B_1 = \alpha(1 - m_f) + (1 - \alpha)(1 - m_f)m_m\bar{p}_{1s}^m - (1 - \alpha)m_f(1 - m_m)\bar{u}_{1s} - 1$$

$$C_1 = m_f\bar{u}_{1s}$$

with the corresponding male equilibrium given by

$$\hat{p}_{1s}^m = \frac{\alpha(1 - m_m)\hat{u}_{1s} + m_m\bar{p}_{1s}^m}{1 - (1 - \alpha)(1 - m_m)\hat{u}_{1s}}. \qquad \text{(E2)}$$

Analysis of the sign of the quadratic (E1) at $u_{1s} = 0$, $u_{1s} = 1$, and as $u_{1s} \to \pm\infty$ shows that when $0 < m_f, \bar{u}_{1s} < 1$ and $0 \leq \alpha, m_m, \bar{p}_{1s}^m < 1$, there is a single, admissible equilibrium solution in (0, 1) for $\hat{u}_{1s}$ and $\hat{p}_{1s}^m$ corresponding to the smaller root of (E1). Also, since

$$f(\bar{u}_{1s}) = -(1 - \alpha)(1 - m_f) \times [1 - m_m\bar{p}_{1s}^m - (1 - m_m)\bar{u}_{1s}]\bar{u}_{1s} < 0$$

and, on (0, 1), $f(u_{1s}) < 0$ if and only if $\hat{u}_{1s} < u_{1s} < 1$,

then $\hat{u}_{1s} < \bar{u}_{1s}$. For males, however, $\hat{p}^m_{1s} > \bar{p}^m_{1s}$ if $\bar{p}^m_{1s} < \bar{u}_{1s}$ and

$$\alpha > \frac{\bar{p}^m_{1s}[1 - m_f\bar{u}_{1s} - (1 - m_f)\bar{p}^m_{1s}]}{(1 - \bar{p}^m_{1s})[m_f\bar{u}_{1s} + (1 - m_f)\bar{p}^m_{1s}]}.$$

Analogous formulas and results hold for the pure species 2 individuals with u_{1s} replaced by w_{2s}, $\bar{u}_{1s}$ by $\bar{w}_{2s}$, p^m_{1s} by q^m_{2s}, $\bar{p}^m_{1s}$ by $\bar{q}^m_{2s}$, and α by β.

As for haplodiploids, the equilibrium for the entire diploid system can be shown to be locally stable if the eight eigenvalues satisfying (A1) all have magnitude less than one. We need only show this holds for the roots of the factors $f_1(\lambda)$ and $f_2(\lambda)$, corresponding to the two pure species, since only the recursions of the pure parental males have changed under the *X*-linked model. Expanding out $f_1(\lambda)$ for the *X*-linked case reveals that its roots are $\lambda_3 = 0$ and

$$\lambda_4 = \alpha(1 - m_f) + (1 - \alpha) \times [(1 - m_f)\hat{p}^m_{1s} + (1 - m_m)\hat{u}_{1s}]. \quad \text{(E3)}$$

The first eigenvalue, λ_3, is obviously less than one, and if we substitute the equilibrium relationship,

$$\hat{p}^m_{1s} = \frac{(1 - m_f)m_m\bar{p}^m_{1s} + (1 - m_m)(\hat{u}_{1s} - m_f\hat{u}_{1s})}{1 - m_f},$$

obtained from (15) and (32) into (E3), we find that $0 < \lambda_4 < 1$ if and only if $\hat{u}_{1s} < -B_1/(2\mathbf{A}_1)$, where, as in the haplodiploid case, this fraction is the critical point of the quadratic defining $\hat{u}_{1s}$ given in (E1). Since $\hat{u}_{1s}$ is the smaller root, this inequality must hold. By symmetry, the roots of $f_2(\lambda)$ also have magnitude less than one. Thus we conclude that the unique, nontrivial equilibrium for the *X*-linked model will be locally stable whenever it exists.