Cytocnuclear Theory for Haploidy 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 cytocnuclear structure for either a cytoclastic and nuclear marker in a haploidy species or a cytoclastic and X-linked marker in a diploid species. Sex-specific disequilibrium statistics that summarize nonrandom cytocnuclear 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 subsampled under the general models. We show that pure type individuals and nonzero cytocnuclear 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 cytocnuclear 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 haploidy or sex-linked cytocnuclear data.

THE study of natural hybrid zones relies heavily on genetic markers and may be greatly aided if both cytoclastic and nuclear DNA markers are available and assayed in each individual (Arnold 1995). The benefit of using such joint data is derived from the fact that cytoclastic DNA is nearly always inherited uniparentally while nuclear DNA is normally inherited biparentally. As a result, cytocnuclear 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 cytocnuclear frequencies and disequilibria for autosomal and cytoclastic 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 1995; Babcock and Asmussen 1996). These frameworks have been applied to cytocnuclear 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; Ayse 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 haploidy 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 cytocnuclear 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 cytocnuclear data may be particularly useful and informative in deducing the evolutionary history of natural populations, in the same way that standard cytocnuclear 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 cytocnuclear systems to include models that describe the expected cytocnuclear structure for haploidy species or X-linked nuclear markers in diploid species. We first define the cytocnuclear 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 cytocnuclear 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...
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 hybridisation. 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 are sub- or superscripted by an *n* for males and an *f* for females, while subscripts of 1 or 2 on frequency variables denote cytonuclear combinations with the *C* or *c* type, respectively. For diploid females, the cytonuclear variables are completely analogous to those under the standard diploid cytonuclear formulation (Amsussen 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 cytopotypes (row sums) and the nuclear genotypes (column sums). From these, we may calculate the nuclear allele frequencies in females as

\[ p_A = \frac{freq(A)}{n} = u + \frac{w}{2} \]

and

\[ q_C = \frac{freq(c)}{n} = w + \frac{u}{2}, \]

where \( q_C = 1 - p_A \). 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, \( p_{ij} = freq(A_i/C_j) \), for instance, is defined as the probability that a random female from the population has cyotype *C* and that a randomly sampled allele at her nuclear locus is *A* (Amsussen and Bassgen 1994).

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

\[ D_1 = \frac{freq(A_1/C_1) - freq(A_2/C_2)}{freq(A_1/C_1) + freq(A_2/C_2)} = u - w \]

\[ D_2 = \frac{freq(A_1/C_2) - freq(A_2/C_1)}{freq(A_1/C_1) + freq(A_2/C_2)} = v - w \]

(1)

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

\[ D_3 = \frac{freq(A_1/C_1)}{freq(A_1/C_1) + freq(A_2/C_1)} = p_A - p_C \]

(2)

that measures the nonrandom association between the nuclear and cytoplasmic alleles in females, where both (1) and (2) for *q* denote the frequency in females. The female cytonuclear disequilibrium statistics are intuitively related by the following equations,

\[ D_2 = D_1 \cdot \frac{p_A}{q_C} \text{ and } D_3 = D_1 \cdot \frac{p_A}{q_C} = 0 \]

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>
<thead>
<tr>
<th>Cytophorety</th>
<th>Nuclear genotype</th>
<th>A</th>
<th>a</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( u_1 = u_1 + \frac{u_1}{2} )</td>
<td>( w_1 = w_1 + \frac{w_1}{2} )</td>
<td>( u_1 = u_1 + \frac{u_1}{2} + \frac{w_1}{2} )</td>
<td>( u_1 + \frac{w_1}{2} )</td>
</tr>
<tr>
<td>c</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( u_2 = u_2 + \frac{u_2}{2} )</td>
<td>( w_2 = w_2 + \frac{w_2}{2} )</td>
<td>( u_2 = u_2 + \frac{u_2}{2} + \frac{w_2}{2} )</td>
<td>( u_2 + \frac{w_2}{2} )</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( u )</td>
<td>( v )</td>
<td>( u + v )</td>
<td>1.0</td>
</tr>
</tbody>
</table>

**TABLE 2**

Frequencies of cytonuclear diallelic combinations in females

<table>
<thead>
<tr>
<th>Cytophorety</th>
<th>Nuclear allele</th>
<th>A</th>
<th>a</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( p_A = u_1 + \frac{1}{2}u_1 = p_A )</td>
<td>( p_A = w_1 + \frac{1}{2}w_1 = p_A )</td>
<td>( p_A = u_1 + \frac{1}{2}u_1 + \frac{1}{2}w_1 )</td>
<td>( p_A )</td>
</tr>
<tr>
<td>c</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( p_A = u_2 + \frac{1}{2}u_2 = p_A )</td>
<td>( p_A = w_2 + \frac{1}{2}w_2 = p_A )</td>
<td>( p_A = u_2 + \frac{1}{2}u_2 + \frac{1}{2}w_2 )</td>
<td>( p_A )</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( \frac{1}{2}p_A )</td>
<td>( \frac{1}{2}p_A )</td>
<td>( \frac{1}{2}p_A )</td>
<td>1.0</td>
</tr>
<tr>
<td>Cytotype</td>
<td>A</td>
<td>a</td>
<td>Total</td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>----</td>
<td>---</td>
<td>-------</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>$p_C^a = p_C a + D_C$</td>
<td>$q_C^a = q_C a - D_C$</td>
<td>$x_C^a$</td>
<td></td>
</tr>
<tr>
<td>c</td>
<td>$p_c a = p_c a - D_c$</td>
<td>$q_c a = q_c a + D_c$</td>
<td>$x_c a$</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>$p_a$</td>
<td>$q_a$</td>
<td>1.0</td>
<td></td>
</tr>
</tbody>
</table>

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

\[ D_C = \text{freq}(A/C) - \text{freq}(A) \times \text{freq}(C) = p_C^a - p_a q_a. \]  

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 cytocnuclear combinations can be written in terms of the relevant sex-specific disequilibrium 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) cytocnuclear 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 inherit 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 cytocnuclear dynamics. Through analysis of a mating table we find that after one generation of mating the frequencies of the joint cytotypic genotypes in females are

\[ u_i = p_i q_i, \quad v_i = p_i q_i + q_i q_i, \quad w_i = q_i q_i, \]  

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

\[ u = p q, \quad v = p q + q q, \quad w = q q. \]  

while the new nuclear and cytoplasmic allele frequencies in females are

\[ p_i' = \frac{1}{2}(p_i + p_e), \quad q_i' = q_i. \]  

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 cytotypic marker. In contrast, the cytotypic 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 cytotypic locus.

We may now use the female frequency recursions (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

\[ D_f = p_f D_f, \quad D_f' = (q_f - p_e) D_f, \quad D_f = q_f D_f. \]  

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 ($p_e, q_e$), and the allelic disequilibrium in the female gamete pool ($D_f$), and are identical to those in the standard, diploid cytoplasmic model when there are frequency differences between the sexes (BARGOCK and ASMUSSEN 1996). Moreover, $D_f$ decays at the same rate as the gametic phase disequilibrium between two unlinked nuclear loci (HEAL and COLKS 1989).

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

\[ p_i' = p_i (q_i') = q_i' \]  

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,

\[ p_e' = p_e, \quad x_e' = x_e, \quad D_e = D_e. \]  

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 the relationships given in Tables 1–3, completely define the cytocnuclear dynamics in the population. To derive these dynamical solutions, define $x'$ as the value of the variable $x$ in any generation $t$ and $x_0'$ as the initial value of $x$. If we further define the initial, overall nuclear allele frequency in the population as $p = \frac{1}{2}p_0 + \frac{1}{2}p_e$, and the initial difference in the nuclear allele frequencies in females and males as $\Delta q_0 = p_0 - q_e$, then the nuclear allele frequencies
in males and females in any generation, \( t = 0, 1, 2, \ldots \), are given by
\[
\begin{align*}
\rho_1^t &= p + \frac{1}{2} \Delta^{(1)} (-\lambda_1^t), \\
\rho_2^t &= p + \frac{1}{2} \Delta^{(2)} (-\lambda_1^t).
\end{align*}
\] (10)

These follow the standard Hardy-Weinberg dynamics for haplodiploid (or X-linked) loci (Hartl and Clark 1989), under which \( p \) and \( q \) both approach the constant, overall nuclear allele frequency, \( p \), in a damped oscillatory fashion. After the first generation, the male-cyto type frequency takes on the frequency in females, and thereafter the cyto type frequencies in both sexes remain at the initial value in females, so that
\[
x_1^t = x_2^t = x_1^0
\]
for \( t = 1, 2, \ldots \). Using the nuclear allele frequency dynamics in (10) and the recursions for the cytonuclear disequilibria statistics in (7) and (9), we can next solve for the values of the four disequilibria at any time \( t \), which are given by
\[
\begin{align*}
\Delta^t &= \rho_1^t \rho_2^t - \frac{1}{2} \Delta^{(1)} (-\lambda_1^t) \Delta^{(2)} (-\lambda_2^t) \\
\Delta^t &= \left( \rho_1^t (1 - \rho_2^t) \right) + \frac{1}{2} \Delta^{(1)} (-\lambda_1^t) \Delta^{(2)} (-\lambda_2^t) \\
\Delta^t &= \Delta^{(1)} (-\lambda_1^t) \\
\Delta^t &= \Delta^{(2)} (-\lambda_2^t).
\end{align*}
\]

As in the standard diploid model (Amsden 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 (Amsden and Basset 1994). The female allelic disequilibrium \( D_{Y} \) decays monotonically with no change in sign, and after the first generation the male cyto type frequency, \( D_{X} \), assumes the value of \( D_{Y} \) lagging one generation behind. In females, the homoygote genotypic disequilibrium, \( D_{Y} \), takes on and retains the sign of the female allelic disequilibrium, while \( D_{X} \) takes the opposite sign of \( D_{Y} \). Heterozygote disequilibrium dynamics not found in the standard diploid model, are possible if initially there are nuclear allele frequency differences between the sexes (\( \rho_1^0 \neq \rho_2^0 \)) and nonrandom allelic associations in females (\( \Delta^0 \neq 0 \)). In particular, under these conditions, it is possible for the female genotypic disequilibrium to increase in magnitude past the first generation. Furthermore, the values of both homoygote disequilibria, \( D_{Y} \) and \( D_{X} \), 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 homoygote disequilibrium, the magnitude of the heterozygote disequilibrium, \( D_{X} \), will also ultimately decay monotonically, but the sign of \( D_{X} \) may exhibit permanent cycling.

![Figure 1](image)

**POPULATION MIXTURE**

Pooling genetically differentiated populations can generate both nuclear and cytonuclear disequilibria in diploid species (Nei and Li 1973; Amsden and Arntz 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 across all \( n \) populations as
\[
\tau = \sum_{i=1}^{n} \frac{x_i}{n},
\] (11)
where \( n_i \) is the fraction from subpopulation \( i \) and \( x_i \) is the value of variable \( x \) in subpopulation \( i \). Then, from (2) and (11) the female allelic disequilibrium in the pooled population is
\[
\Delta^F = \Delta^X - \sum_{i=1}^{n} \frac{x_i}{n} \Delta^X + \sum_{i=1}^{n} \frac{x_i}{n} \Delta^X = \Delta^X + \sum_{i=1}^{n} \frac{x_i}{n} \Delta^X,
\]
Similar calculations for the female genotypic disequilibria, \( D_{Y} \), and male allelic disequilibrium, \( D_{X} \), show that in the combined population
\[
\Delta^F = \Delta^X + \sum_{i=1}^{n} \frac{x_i}{n} \Delta^X = \Delta^X + \sum_{i=1}^{n} \frac{x_i}{n} \Delta^X;
\]
where \( g = u, v, o \) for \( i = 1, 2, 3, \ldots \), respectively. These results mirror those found under the standard diploid formalism, in that each total disequilibrium is the weighted average of the values in the subpopulations plus the covariance between the cyto type frequency and
the appropriate nuclear frequency across the subpopu-
lizations (Asmussen and Arnold 1991). The coance-
tance terms have a particularly nice interpretation in the spe-
cial case when just two subpopulations are pooled, for
which the admixture formulas become
\[ D_f^2 = D_f + m_1(1 - m_1)(g_1^2 - g_0^2)(s_1^2 - s_0^2) \]
\[ D_f^2 = D_f + m_1(1 - m_1)(g_1^2 - g_0^2)(s_1^2 - s_0^2) \]
\[ D_e^2 = D_e + m_1(1 - m_1)(g_1^2 - g_0^2)(s_1^2 - s_0^2), \]
(12)
where, once again, \( g = g_u, v \), \( s = s_u, v \) for \( i = 1, 2, 3 \), re-
respectively. In this instance, the coancestries are nonzero, and there is a cyto
cnuclear admixture effect in that the total dis-
queility differs from the mean of the values in the
subpopulations, if and only if the cyto-
type and the asso-
ciated 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 HAPLOIDPILOTS

In this section we develop models that explore the
effects of hybridization on the cytonuclear struc-
ture of haploidploid species. We assume that individu-
als from two genetically differentiated populations continuously
migrate into a zone of admixture where mixing occurs.
Although our model is more general, we are primarily
interested in hybrid zones where the source popula-
tions are fixed for alternate alleles. In this case, source
population 1 (species 1) will be composed only of fe-
males of genotype A/A or C/C and males of genotype A/C,
while source population 2 (species 2) is composed only
of females of genotype a/a 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 pa-
rental individuals at the two-locus level. As in previous
diploid formulations (Arndt et al. 1986; Asmussen et
al. 1989), it is useful to divide these homospecific classes
into subclasses based on their true species status. Fe-
males that display genotype A/A, for example, may
be either pure parentals from source population 1 (freq
\( u_2 \)), or they may be hybrids (freq \( u_1 \)). We may subdi-
vide the other homospecific classes in similar ways to
obtain the four partitions,
\[ u_2 = u_1 + u_2, \quad u_0 = u_0 + u_1, \]
\[ p_2 = p_2 + p_2, \quad q_2 = q_2 + q_2, \]
where the subscript \( r \) represents a pure species individ-
ual and the subscript \( h \) represents a hybrid. In practice, these
subspecies may be distinguished from one another with a high degree of confidence through the examina-
tion of multiple diagnostic nuclear loci in conjunction
with a diagnostic cytoplasmic marker.

Interestingly, the dynamics of the pure species indi-
viduals in the haploidploid and the diploid, X-linked
models deviate due to the differing modes of male pro-
duction. Haploidploid males are produced parthenoge-
 netically; 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 type female mates with a conspecific male
(since all sexually produced sons receive half their au-
tosomal complement from their father, which, al-
though not monitored, nonetheless affect their true
species status). Pure type females are not affected in
the way since both the haploidploid 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 haploidploid. The differences that
arise when considering an X-linked marker in a diploid
species will be dealt with in the CONTINENT-ISLAND MOD-
ELS 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 conspe-
ic male with probability \( a \) and mate at random with
probability \( 1 - a \). Similarly, a pure species 2 female
will preferentially mate with a conspecific male with
probability \( \beta \) and mate at random with probability \( 1 - \beta \).
The other six hybrid type females are assumed to
always mate at random. Our formulation includes ran-
mating as a special case corresponding to \( a = 0 = \beta \)
(see below).

We assume that every generation a constant fraction,
\( m_0 \), of females within the hybrid zone are migrants from
source population 1, and a constant fraction,\( m_0 \), of females are migrants from source population 2, while the remaining fraction of females \( 1 - m_0 \), are offspring of previous residents. Males may mi-
grate into the hybrid zone at different rates from the
females so that every generation, a fraction \( m_0 \) and
\( m_2 \) 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 vari-
bles in the male and female migrant pools as \( p_2, p_u, p_3, q_2, q_u, q_3 \), etc. For all frequencies this overall value is
simply the arithmetic average of the corresponding fre-
duencies in the two source populations weighted by the
appropriate sex-specific migration rate. For example, if
the cyto type frequency in females is \( s_2 \) and \( s_0 \) in
source populations 1 and 2, respectively, then the fe-
male cyto type frequency in the migrants is \( s = \frac{m_0s_0 + m_2s_2}{m_0 + m_2} \). The cytonuclear dis-
equilibrium in the migrant pools can be computed from
g their definitions (e.g., \( D = s - \mu y_0 \) or from the
admixture formulae in (12). In the special case of in-
erest, where the two source populations are fixed for at-
terrate alleles, the frequencies and disequilibrium in the
migrants are simple functions of the sex-specific migration rates, with
\[ a_i = \frac{a_i}{b_i} = \frac{y_i}{y_j} = \frac{m_i^{(2)}}{m_j} \]
\[ b_i = \frac{b_i}{b_j} = \frac{z_i}{z_j} = \frac{m_j^{(2)}}{m_i} \]
\[ e_i = \frac{e_i}{e_j} = \frac{k_i}{k_j} = \frac{d_i}{d_j} = \frac{n_i}{n_j} = D_i = 0 \]
\[ D_i = D_{i-1} = \frac{m_i^{(2)} n_j^{(2)}}{(m_j)^2} \]
(17)
in females, where \( m_j = m_j^{(1)} + m_j^{(2)} \) is the total female migration rate, and
\[ f_i = \frac{f_i}{f_j} = \frac{r_i}{r_j} = \frac{m_i^{(1)}}{m_j} \]
\[ g_i = \frac{g_i}{g_j} = \frac{q_i}{q_j} = \frac{m_j^{(1)}}{m_i} \]
\[ f_i = \frac{f_i}{f_j} = \frac{r_i}{r_j} = \frac{m_i^{(1)}}{m_j} \]
\[ D_i = D_{i-1} = \frac{m_i^{(1)} n_j^{(1)}}{(m_j)^2} \]
(14)
in males, where \( m_j = m_j^{(1)} + m_j^{(2)} \) 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 recurrences: 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 cytonuclear 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, \( m_j \). Through analysis of a mating table, it can be shown that the resulting recursions for the two parental female classes are
\[ u_i = n_i u_i + (1 - n_i) u_j (\alpha + (1 - \alpha) p_j) \]
\[ u_j = n_j u_j + (1 - n_j) u_i (\beta + (1 - \beta) p_i) \]
(15)
while those for the six basic female cytonuclear genotypes are
\[ u_i^{(1)} = n_i u_i^{(1)} + (1 - n_i) \left[ (p_i q_i + q_i p_i) x_i \right] \]
\[ + \left( q_i - q_i p_i \right) y_i - a_i u_i^{(2)} \]
\[ u_j^{(1)} = n_j u_j^{(1)} + (1 - n_j) \left[ (p_j q_j + q_j p_j) y_j \right] \]
\[ - \left( q_j - q_j p_j \right) x_j - \beta u_j^{(2)} \]
(16)

For ease of analysis, we have expressed the female recurrences 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 diacylic combinations (e.g., the new frequency of the AA/C genotype is
\[ u_i^{(1)} = n_i u_i^{(1)} + (1 - n_i) \left[ (p_i q_i + q_i p_i) \right] \]
\[ u_j^{(1)} = n_j u_j^{(1)} + (1 - n_j) \left[ (p_j q_j + q_j p_j) \right] \]
(17)
and the new female allelic frequencies are thus
\[ p_i^{(1)} = n_i p_i^{(1)} + (1 - n_i) (p_i q_i + q_i p_i) \]
\[ q_i^{(1)} = n_i q_i^{(1)} + (1 - n_i) (q_i p_i + p_i q_i) \]
(18)

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

The new values of the four female cytonuclear \( \alpha_i \)...
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, 

$$E_i = m_i D_i + (1 - m_i) p_i D_i + \alpha u_i \phi_i \psi_i + \psi_i (1 - m_i) p_i D_i + \alpha u_i \phi_i \psi_i$$

(19a)

$$E_i = m_i D_i + (1 - m_i) (q_i - p_i) D_i + \psi_i (1 - m_i) p_i D_i + \alpha u_i \phi_i \psi_i$$

(19b)

$$E_i = m_i D_i + (1 - m_i) (q_i - p_i) D_i + \psi_i (1 - m_i) p_i D_i + \alpha u_i \phi_i \psi_i$$

(19c)

$$E_i = m_i D_i + \frac{1}{2} (1 - m_i) D_i + \alpha u_i \phi_i \psi_i + 2\alpha u_i \phi_i \psi_i$$

(19d)

As in the standard diploid formulation (Adusumil et al. 1989), the native 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 males, weighted by the total male migration rate. The recursions for the male genotypic frequencies are thus

$$\begin{align*}
(p_i') &= m_i p_i + (1 - m_i) q_i \\
(q_i') &= m_i q_i + (1 - m_i) p_i \\
(\phi_i') &= m_i \phi_i + (1 - m_i) \psi_i \\
(\psi_i') &= m_i \psi_i + (1 - m_i) \phi_i
\end{align*}$$

(20)

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

$$p_i' = m_i p_i + (1 - m_i) p_i'$$

$$q_i' = m_i q_i + (1 - m_i) q_i'$$

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

$$E_i = m_i D_i + (1 - m_i) D_i$$

$$+ \alpha u_i (1 - m_i) (q_i - p_i) (\psi_i - \phi_i).$$

(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 cytoplasmic system with $0 < \hat{u}, \hat{u}, \gamma, \beta < 1$ if $0 < \beta, \beta, \gamma, \beta, \gamma < 0$, and this equilibrium can be shown to be locally stable whenever it exists (see Appendix A). The equilibrium frequencies of the pure parental females, $u_i$ and $u_i$, 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, $p_1$ and $p_2$, are then simply obtained from the (reversion) relationships in (20). We find that, as in the standard, diploid formulation (Adusumil et al. 1989), $u_1 < u_2$ and $u_1 < u_2$. This 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., $p_i$ can exceed $p_i$ if $u_i > u_i$). Derivations of these pure specics results can be found in Appendix B.

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

$$x_i(t) = x_i + (x_i(t) - x_i) (1 - m_i) x_i$$

(22)

and

$$x_i(t) = x_i + (1 - m_i) x_i$$

$$+ (1 - m_i) (x_i(t) - x_i) (1 - m_i)^{i-1}$$

$$x_i(t) = x_i + (1 - m_i) x_i$$

(23)

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

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

$$\begin{align*}
\hat{p} &= \frac{2m_i p_1 + (1 - m_i)}{2m_i + (1 - m_i)} \\
\hat{q} &= \frac{2m_i q_1 + (1 - m_i)}{2m_i + (1 - m_i)} \\
\hat{\phi} &= \frac{m_i \phi_1 + (1 - m_i) \phi_1}{m_i + (1 - m_i) (\alpha u_i + \beta u_i)} \\
\hat{\psi} &= \frac{m_i \psi_1 + (1 - m_i) \psi_1}{m_i + (1 - m_i) (\alpha u_i + \beta u_i)}
\end{align*}$$

(24)
\[ f_x = \frac{(1 + m_0) \beta_x + (1 - m_0) \alpha_x}{2m_0 + (1 - m_0)} \times \frac{(1 - m_0)(\alpha_x \beta_x + \beta_x \alpha_x)}{m_0 + (1 - m_0)(\alpha_x + \beta_x \alpha_x)} \]  

(25) 

Due to the effects of assortative mating in the resident population, these values are not simple weighted averages of the migrant values, \( \beta_x \) and \( \alpha_x \). 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 (\( m_0 = 0 \) or \( m_0 = 1 \)).

The equilibrium for the female allele association, \( \hat{D}_f \), can now be found by inserting (22), (24), (25), and \( \alpha_x \) and \( \beta_x \) from APPENDIX B into (19d) and solving for the steady state, giving:

\[ \hat{D}_f = \frac{2m_0 \beta_x + (1 - m_0) \alpha_x \beta_x}{2m_0 \alpha_x + (1 - m_0) \beta_x \alpha_x} \]

(28) 

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

\[ \hat{D}_l = \frac{m_0 \beta_x + (1 - m_0) \alpha_x \beta_x}{2m_0 \alpha_x + (1 - m_0) \beta_x \alpha_x} \]

\[ \hat{D}_u = \frac{m_0 \alpha_x + (1 - m_0) \beta_x \alpha_x}{2m_0 \beta_x + (1 - m_0) \alpha_x \beta_x} \]

(29a)

(29b)

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

\[ \beta_{x-m} = m_0 \beta_x + (1 - m_0) \beta_x \]

\[ + \frac{m_0 \alpha_x + (1 - m_0) \beta_x}{2m_0 \beta_x + (1 - m_0) \alpha_x \beta_x} \]

(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 cytochrome frequencies are the same for both sexes (\( \bar{e} = \bar{e}_x \)) or the equilibrium nuclear allele frequency in females is equal to the nuclear allele frequency in migrant males (\( \bar{e}_x = \beta_x \)). The equilibria for the remaining variables are found by substituting the appropriate equilibrium values given above into the recurrences in (16), (17), and (20).

There are four notable points regarding the steady-state values of the cyto-nuclear disequilibria within the hybrid zone. First, any female migration will generate permanent cyto-nuclear disequilibria in both sexes if there are non-random 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 non-random associations in males. Second, parallelizing the standard diploid model (AMMSEN et al., 1989), if the source populations are fixed for alternate nuclear and cytoplasmic alleles, the final female disequilibria satisfy \( \hat{D}_f < 0 \) if \( \hat{D}_f \) with the sign of \( \hat{D}_l \) 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., \( 0 < \hat{D}_l < \hat{D}_f \)) since, with diagnostic markers, \( \bar{e}_x < \bar{e} \) and \( \bar{e}_x < \bar{e}_x \), as \( \bar{e}_x \) is fixed and hence, in the numerator of (26), \( \alpha_x \beta_x \beta_x + \beta_x \alpha_x \beta_x < \alpha_x \beta_x \beta_x + \beta_x \alpha_x \beta_x = \hat{D}_f \). Finally, due to the close dependence of males upon females, the sign of \( \hat{D}_f \) 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, \( \hat{D}_f \) and \( \hat{D}_u \).

Specific case \( \bar{e}_x = \bar{e} \) and \( m_0 = 0 \). If all individuals in the hybrid zone mate at random (\( \alpha = \beta = 0 \)), several additional details of the cyto-nuclear system may be discerned. For example, in addition to the time-dependent solutions for the cyto-type frequencies given in (22) and (23), it is possible to obtain the dynamical solutions for \( \bar{e}_x, \bar{e}_y, \) and \( \bar{e}_x \) (APPENDIX C), which fully determine the cyto-nuclear dynamics for all but the frequencies of the pure species individuals. The equilibrium for the nuclear allele frequencies are now simply weighted averages of the frequencies in the migrant males and females (\( \beta_x, \beta_x \)), with:

\[ \beta_x = \frac{2m_0 \beta_x + (1 - m_0) \alpha_x \beta_x}{2m_0 \alpha_x + (1 - m_0) \beta_x \alpha_x} \]

(30)

Thus, in random mating zones, the nuclear allele frequency will equilibrate in the two sexes if and only if \( \beta_x = \beta_x \), in which case the values in both sexes converge to the common migrant value (\( \beta_x = \beta_x \)). 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 geographic rate, 1 - \( m_0 \) for the cyto-types depending on whether the female migration rate (\( m_0 \)) is less than, equal to, or greater than the male migration rate (\( m_0 \)).

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

\[ \hat{D}_l = \frac{2m_0 \beta_x}{1 + m_0} \]

which is approached at the asymptotic rate of 1 - \( m_0 \) per generation. The equilibrium allelic association in males (\( \hat{D}_u \)) in (27) also simplifies due to the fact that

\[ \hat{D}_u = \frac{2m_0 \beta_x}{2m_0 + (1 - m_0) m_0} \]

is now just a constant multiple of \( \beta_x \). Consequently, within random mating zones, there is an admixture effect upon \( \hat{D}_u \), only if the migrant nuclear and cytoplasmic
frequencies both differ between the sexes ($f_b = f_a$ and $f_y = f_a$).

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

No migration ($m_y = m_a = 0$): Such a situation may occur if an established hybrid zone becomes disconnected from its source population(s). This results in a significantly different cytonuclear disequilibrium, 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 important 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., $x^{(t)}_y = x^{(0)}_y = x^{(0)}_y$ for $t = 1$).

The two remaining distinctions of this case stem specifically from the absence of migration by pure parents and males. On the one hand, the lack of input of pure parents means that their frequencies will decay to zero provided that assortative mating is incomplete ($0 < a, b < 1$). 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 disequilibrium 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 frequencies in males and females will not necessarily be the overall initial values, $p = \frac{1}{2} m_y + \frac{1}{2} m_a$, 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 ($0 < m^{(1)}_y < 1, m^{(1)}_a < 1; m^{(0)}_y = m^{(0)}_a = 0$): 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 parents. Although fixation for the incoming pure types is a valid equilibrium state, it is unstable (see APPENDIXES A and B) if

$$
\begin{align*}
\alpha < 1 & \quad m_y \quad \text{and} \quad m_a < \frac{1}{2} - m_a < \frac{1}{2} \\
\end{align*}
$$

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

$$
\begin{align*}
\omega_y &= \frac{m_y}{(1 - a)(1 - m_y)(1 - m_a)} < 1 \\
\end{align*}
$$

and

$$
\begin{align*}
\omega_a &= \frac{m_a + (1 - a)(1 - m_y) m_a}{(1 - a)(1 - m_y)} < 1 \\
\end{align*}
$$

with $\omega_y = \omega_a = 0$. 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 ($m_a = 0, 0 < m_y < 1$): If only males migrate into the hybrid zone and assortative mating is incomplete ($0 < a, b < 1$), 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 $0 < \beta_1, \beta_2 < 1$) at frequencies of $m^{(1)}_y$ and $m^{(1)}_a$, 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., $x^{(t)}_y = x^{(0)}_y$ for all $t \geq 0$), and the cytoplasmic frequency in males will immediately stabilize at

$$
\omega_y = m_y \omega_a + (1 - m_y) \omega_y^{(0)},
$$

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 ($\omega_y^{(0)}$). 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 $\omega_y = m_y \omega_y^{(0)}$ 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 ($0 < m_y < 1, m_a = 0$): When males do not migrate into the hybrid zone, all male
cytenucleai variables will always equal the analogous female values in the previous generation (e.g., \( P_{ij}^0 = P_{ji}^0 \)), and therefore each male equilibrium will equal in counterpart to females (e.g., \( g_i^0 = q_i^0 \), \( \Delta_i = \delta_i = \xi_i \)). 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 (\( m_i^0 = m_i^0 = m_i^0 = m_i^0 \)) and \( m_i^0 = m_i^0 \):** The only real simplification comes when the cytenucleai frequencies are the same in the male and female migrants (e.g., \( u_i = u_i \), \( h_i = h_i \), \( B_i = B_i \)), as occurs if the two source populations are fixed for alternate alleles. In this case, the cytenucleai frequencies in both sexes equilibrate after the first generation (\( u_i^0 = u_i^0 \) for all \( i = 1 \)) and monotonically approach the migratcytenucleai frequency (\( x_i = x_i \)). The final male disequilibrium is \( \Delta_i = m_i^0 \Delta_i + (1 - m_i^0) \Delta_i \), which is a simple weighted average of the male disequilibrium in the migrants (\( \Delta_i = \Delta_i \)) and the final allelic association is females, weighted by the total migration rate in each sex (\( m = m_0 \equiv m_0 \)).

**Effect of census times:** 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 cytenucleai plakder. The important parallel is that the only variable whose equilibrium and dynamics are the same under both census schemes is the female cytenucleai frequency (\( x_i \)), which, in both cases, converges monotonically to the value in the migrant females (\( x_i \)) at the constant rate of 1 - \( m_i^0 \) per generation. The major contrast is that, under census 2, the cytenucleai frequency in males will equal that in females after one generation, while under census 1 the two sexes have distinct cytenucleai plastic frequency dynamics. With the exception of the cytenucleai frequency in females, all frequency variables at each census after migration and before mating (\( x_i \)), and the previous census before migration and after mating (\( x_i \)) are simply related to one another by an equation of the form

\[ x_i^0 = m_i x_i + (1 - m_i) x_i \]  

(29)

for all \( i = 1 \), where \( x_i \) is the overall value of the variable in the sex-specific migrant pool. This equation holds for all female frequency variables with \( m_i \) replaced by \( m_i \) and for all male frequency variables with \( m_i \) substituted for \( m_i \). At equilibrium, the same relationship

\[ x_i = m_i x_i + (1 - m_i) x_i \]  

(30)

applies to all variables but the male allelic disequilibrium (\( \Delta_i \)). The relationship between the latter under the two census schemes is less simple and is given by

\[ \Delta_i = m_i \Delta_i + (1 - m_i) \Delta_i + m_i(1 - m_i) (g_{ij}^0 - n_{ij}^0) (x_i - x_i) \]  

(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., \( g_{ij}^0 = g_{ij}^0 \)). Thus, all male equilibrium under census 2 will equal those female counterparts under census 1 (i.e., \( g_{ij}^0 = g_{ij}^0 \)). Like mating at another way, with the exception of the cytenucleai 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 \( g_{ij} \). \( g_{ij} \). and \( g_{ij} \)). For example, as in the standard diploid model (AAMERSFEN et al. 1989) only three relationships are possible when comparing a value in the migrants (\( z_i \) and the corresponding equilibria under census 1 (\( z_i \)) and census 2 (\( z_i \))):

- \( z_i < z_i < z_i \) or \( z_i < z_i < z_i \) or \( z_i = z_i = z_i \)

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 D**), censuing 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 necessarily less than that in the female migrants (\( \Delta_i < \Delta_i \)); the relationships for the other dimorphic alleles are not as simple and depend on the migration rates and assortative mating parameters.

**CONTINENTAL 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 a constant sequence, the X-linked analogous of (30) we as follows:

\[ g_{ij}^0 = m_i g_{ij}^0 + (1 - m_i) g_{ij}^0 (1 - a) g_{ij}^0 \]  

(32)

These are the only variables whose recursions differ between the two systems; however, this difference gen-
eraly affects the dynamics of the pure species females and the time-dependent values of all variables except the two cytophore frequencies if the pure species individuals mate assortatively ($a = 0$ or $b = 0$). Turning to the steady state of the $X$linked system, we find that a unique, locally stable equilibrium exists with $0 < q$, $q$, $q$, $q$, $P_c$, $P$, $P$, $< 1$ if $0 < m$, $m$, $m$, and $m$, respectively (see APPENDIX E). Although the equilibria of both pure females and males (presented in APPENDIX E) differ from the haplodiplont model, the qualitative relationships to their corresponding frequencies in the migrant pool are still satisfied (i.e., $q < q$ and $q < q$, but $P$ and $P$, not necessarily less than $P$ and $P$ respectively). The equilibrium formulas for all other variables take on the same forms as in the haplodiplont model, but (with the exception of the cytophore frequencies) the actual final values differ due to their dependence on the equilibrium frequencies of the pure parents if there is assortative mating.

A numerical analysis conducted by choosing values of $m$, $m$, $P$, $P$, $P$, $P$, $P$, and $b$ 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 haplodiplont 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 haplodiplont system. Thus, under the haplodiplont 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 haplodiplont models when the pure species mate at random ($a = b = 0$), 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 ($m = m = 0$):** 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., $P^{(0)}_c = P^{(0)}$ and $P^{(0)} = P^{(0)}$).

Migration from only one population ($0 < m$: $m = 0$): 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 ($q = P = 1$) is unstable (see APPENDIX E) if $m < 1 - m$ and $a < 1 - m = m$. and the frequencies of pure individuals within the hy-
DISCUSSION

We have developed the first theoretical frameworks necessary to analyze the cytonuclear structure for haploidloid species or for 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 (Amsunen et al. 1987) in that for diacile markers there are six joint genotypes, with one allitic 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 (Amsunen et al. 1987, Amsunen and Basten 1994, 1996, Dean and Arnold 1995, Basten and Amsunen 1996). The genetic architecture of haploid males, however, deviates from the standard, cytonuclear framework in that for diacile markers there are only four joint genotypes and only a single, allitic disequilibrium. Because the structure of the male data parallels that of genetic data from purely nuclear systems, estimates and significance of male disequilibria can be obtained via established methods for analyzing two-locus genetic phase disequilibrium from nuclear haplotype data (Wra 1996).

As a first step toward understanding and interpreting observed cytonuclear associations in haploidoid and X-linked systems, we analyzed the dynamical behavior of their disequilibria under Hardy-Weinberg conditions. A major finding is that the male allitic disequilibrium ($D_{m}$) lags one generation behind, and takes on twice the value of, the allitic disequilibrium in females ($D_{f}$) after the first generation of random mating. Furthermore, $D_{m}$ and the female homoygote disequilibrium, $D_{n}$, immediately take on and retain the initial sign of $D_{f}$, while the alternate female homoygote disequilibrium, $D_{v}$, takes on the opposite sign. This sign pattern parallels that found in the standard diploid model (Amsunen et al. 1987), except here the signs depend solely on the initial female allitic 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 haploidloid species or for 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 sexspecific disequilibria 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 cyto

nuclear 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 haploidloid 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 cytonuclear 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 cyto 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 easier 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 equilibria sign pattern parallels that found in the Stan-
Cytoskeletal Disequilibria

dard, diploid system (Asimussen et al. 1989) in that under
esis of males, the female allele of disequilibrium and
the homoygote disequilibrium, Δh, will both be pos-
tive, while the alternate homoygote disequilib-
rium, Δp, is negative; the sign of the heteroygote dis-
equilibrium, Δs, is variable and depends on the migra-
tion and assortative mating parameters. Also, with fixed
 differences between the sources, the female allelic asso-
ciation for hybrid zones may still be less than be-
that in the migrants (0 \( < Δs < Δh \)). In contrast to the
disequilibrium patterns found in the females, only un-
der census 2 are we ensured that the sign of the single,
males all disequilibrium (Δh) will be positive with
high diagnostic markets. 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 be-
come fixed for the pure species arriving from the single
source population, even though all individuals will be-
come fixed for its alleles at a loci. The reason for this
apparent paradox is that some of the resident individu-
als are distantly derived from hybrids so they are not
considered pure by one strict definition, although they
would be indistinguishable from pure type individuals
genetically. Furthermore, results from some of the spe-
cial cases may be useful in detecting patterns of migra-
ation in hybrid zones. Migration of only males can be
detected by examination of the frequency of pure pa-
rental 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 usu-
ally differ under census 2.

Another discovery of considerable practical impor-
tance is that separate models are needed to analyze
hybrid zone data from haploids/ploids and X-Inked sys-
tems when pure type individuals are distinguished. This
dichotomy results from the fact that males are produced
parthenogenetically in haploids/ploids species whereas
they are produced sexually in diploid species, thereby
yielding distinct dynamics for the pure species males.
Although the recissions and qualitative behavior for all
of the other variables in the X-Inked system are identi-
cal to those for haploids/ploids, 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
 assortatively. One important result stemming from the
distinction between the X-Inked and haplo-
pliod models is that the equilibrium frequency of pure
parental males and females will both be higher under
the haploids/ploids model for identical parameter values.

Another noteworthy difference is that, under the X-
in line for only one, the frequencies of the pure
parental males and females will be identical when cen-
susng after mating but before migration (census 2), but
usually differ when censusing directly after migration
(census 1). For the haploids/ploids model, the frequencies
of the pure parents 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 cen-
sus 1.

The models that we have developed can be used to
estimate sex-specific rates of migration and assortative
mating by pure parents within a hybrid zone by ex-
tending the maximum likelihood methods developed for
the standard, diploid formulation (Asimussen et al.
1989). We wished to assess these values in an area of
hybridization between two haploids/ploids species, So-
lospis inoita and S. richeri. These two pests were intro-
duced earlier this century, and they now form a large
hybrid zone that spans across much of northern Ala-
bama, Mississippi, and Georgia (Vinson and Green-
berg 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) (Marken et al. 1972).
Therefore, the 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. The method was extended to expand the
models to incorporate the effects of population struc-
ture within hybrid zone 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 HAPLOID MODELS UNDER CENSUS 1

The cytocline recursions for census 1 depend on only eight variables: \(u, \bar{p}, \bar{q}, u_0, \bar{p}_0, \bar{q}_0, D_0\), and \(\alpha\). Therefore, the equilibrium for the eaze 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

\[
\frac{D\lambda}{D\lambda} - \lambda = 0
\]

(\(\lambda\) is the characteristic equation for the pure species 1 subsystem \((u, \bar{p}, \bar{q})\) and \(\lambda\) is the analogous characteristic equation for the pure species 2 \((u_0, \bar{p}_0, \bar{q}_0)\), and all partial derivatives are evaluated at the equilibrium. The first two eigenvalues, \(\lambda_1 = \frac{D\lambda}{D\lambda} = 1 - |\mu|\) and \(\lambda_2 = \frac{D\lambda}{D\lambda} = \frac{1}{2} (1 - |\mu|)\), will be less than one in magnitude provided that all females in the hybrid zone are not replaced each generation \((|\mu| < 1)\).

The three remaining factors of \((\lambda_1)\) are all quadratics of the form \(f(x, \lambda) = x - A_1 \lambda + B_1\) with \(A_1 > 0\) and real roots (since in each case \(A_1 - 4B_1 > 0\)). The roots of such equations lie in \([-1, 1]\). If and only if \(A_1 < 2\) and \(A_1 < 1 + \beta\) (Goldberg 1958). Expansion of the first quadratic shows that

\[
A_1 = 1 - \mu^2/2 + \alpha (1 - \alpha) \mu \bar{p}_0
\]

and

\[
B_1 = -\left(1 - \alpha \mu\right)(1 - \mu) \left(1 - \bar{m}_0 \right) \bar{q}_0
\]

where \(\bar{p}_0\) and \(\bar{q}_0\) are given by (B2) and the smaller solution of (B1).

\[
A_1 < 1 \leq A_1 < 1 + \beta\]

Also, \(\mu_0\) is the smaller of the two roots of this quadratic. (A3) must hold whenever the equilibrium exists. Analogous arguments show that the eigenvalues, \(\lambda_2\) and \(\lambda_3\), obtained from the second quadratic factor, \(\lambda_2(\lambda)\), of \((\lambda_1)\) always lie in \([-1, 1]\). The coefficients of the final factor, \(\lambda_3(\lambda)\), is

\[
\lambda_3 = \frac{1}{2} (1 - \mu_0)
\]

and

\[
\lambda_3 = -\frac{1}{2} (1 - \mu_0) - \left(1 - \bar{m}_0\right) \left(1 - \bar{m}_0\right) \bar{q}_0
\]

Since all eigenvalues are less than 1 in magnitude, the equilibrium is locally stable.

APPENDIX B
EQUILIBRIUM FREQUENCIES OF HAPLOID MODELS UNDER CENSUS 1

Inspection of the recursions for \(u_0\), \(\bar{q}_0\) given in (15) and (20) shows that at equilibrium \(\bar{q}_0\) must satisfy

\[
f(u_0) = A_2 u_0^2 + B_2 u_0 + C_2 = 0
\]

(\(B_1\)) with the corresponding male equilibrium given by
\[ p_i^n = m_n f_i^n + (1 - m_n) s_i, \quad (B2) \]

When \( 0 < m_n, s_i < 1 \) and \( 0 < \alpha, m_n < 1 \), then \( f(0) > 0, f(1) < 0, \) and \( f(u_n) > 0 \) as \( u_n \to -\infty \); thus, in this case there is always exactly one solution, \( u_n = u_n \), in the admissible range of \( 0 < u_n < 1 \), which is given by the smaller root of \( (B1) \). Furthermore, since

\[ f'(u_n) = -\left(1 - \alpha \right) \left(1 - m_n u_n \right)^{1/2} \left(1 - m_n u_n \right)^{-1/2}, \]

and, on \( (0, 1) \), \( f'(u_n) > 0 \) if and only if \( s_i < u_n < 1 \), then it must always be true that \( s_i < u_n \). This relationship is not necessarily true for pure type males, for which \( f'_n > f'_n \), if \( f'_n < s_i \), and

\[ a > 1 - \frac{m_n (u_n - f'_n)}{f'_n (1 - f'_n)}, \]

Analogous formulas and results hold for the pure species 2 individuals with \( u_n, s_i, f'_n, f'_n, s_i \) replaced by \( u_n, s_i, f'_n, f'_n, s_i \) and \( \alpha \) by \( \beta \).

APPENDIX C

TIME-DEPENDENT SOLUTIONS FOR HAPLOIDOPLOIDS UNDER CENSUS 1 AND RANDOM MATING

Solutions for \( p_i^{(0)}, p_i^{(d)} \) and \( D_i^{(d)} \) at any time \( t \) can be obtained in the special case of random mating populations. The normal difference dynamics take the form of \( p_{i+1} = A p_i + b \) where \( p_i = (p_i^{(0)}, p_i^{(d)})^T, b = (m_1 f, m_2 f)^T, \) and the coefficient matrix \( A \) is

\[ A = \begin{pmatrix} \frac{1}{2} (1 - m_n) & \frac{1}{2} (1 - m_n) \\ 1 - m_n & 1 - m_n \end{pmatrix}. \]

Iterating this matrix recursion yields the solution

\[ p_i = A^t p_0 + \sum_{n=0}^{t-1} A^n b \quad \text{for} \quad t = 1, 2, \ldots, \]

where \( A^n = I \) is the \( 2 \times 2 \) identity matrix. Using the spectral decomposition of the matrix \( A \), this simplifies to

\[ p_i = P \Lambda^t p_0 + \sum_{n=0}^{t-1} P \Lambda^n b. \]

Here,

\[ \Lambda = \begin{pmatrix} \alpha & 0 \\ 0 & \lambda \end{pmatrix}, \]

where

\[ \alpha = 1 - m_n \sqrt{(1 - m_n) (9 - 2 m_n)} \quad \text{and} \quad \lambda = \frac{1}{2} (1 + \frac{1}{m_n} (9 - 2 m_n)) \]

are the two eigenvalues of the matrix \( \Lambda \),

\[ P = \begin{pmatrix} \lambda_1 & \lambda_2 \\ 1 - m_n & 1 - m_n \end{pmatrix}, \]

and

\[ P^T = \begin{pmatrix} \lambda_1 & -\lambda_2 \\ -\lambda_1 & \lambda_2 \end{pmatrix}, \]

where the columns of the matrix \( P \) are the right eigenvectors of the matrix \( \Lambda \) corresponding to \( \lambda_1 \) and \( \lambda_2 \). After considerable algebra, we find that in any generation \( t = 1, 2, \ldots \),

\[ p_i^{(0)} = \frac{(1 - m_n) p_i^{(0)} + \lambda_i p_i^{(d)}}{\lambda_i - \lambda_j} \quad \text{and} \quad p_i^{(d)} = \frac{(1 - m_n) p_i^{(d)} + \lambda_j p_i^{(0)}}{\lambda_j - \lambda_i}, \]

where \( \lambda_1 \) and \( \lambda_2 \) are the equilibrium nuclear allele frequencies given in (28),

\[ \lambda_1 = \frac{(1 - m_n) p_i^{(0)} + \lambda_i p_i^{(d)}}{\lambda_i - \lambda_j} \]

and \( \lambda_2 = \frac{(1 - m_n) p_i^{(d)} + \lambda_j p_i^{(0)}}{\lambda_j - \lambda_i} \)

for \( i = j = 1 \), and for \( p_i^{(0)} \), \( p_i^{(d)} \), and \( D_i^{(d)} \) are the initial nuclear allele frequencies in females and males. For both \( p_i^{(0)} \) and \( p_i^{(d)} \), the dominant factor is \( \lambda_i \) corresponding to the larger of the two eigenvalues. Under random mating, the female allelic disequilibrium recursion reduces to

\[ D_i^{(d)} = \frac{(1 - m_n) p_i^{(0)} + \lambda_i p_i^{(d)}}{\lambda_i - \lambda_j} \times \left( p_i^{(0)} + p_i^{(d)} - 2 \frac{\bar{f}_j}{\bar{f}_j} (s_i^{(0)} - \bar{s}_i) + m_1 D_i \right). \]

After substituting in the time-dependent solutions for the allele frequencies given in (22) and (23), we find that (C4) has the form

\[ D_i^{(d)} = a D_i^{(d)} + a_1 d_1^{(d)} + a_2 d_2^{(d)} + a_3 d_3^{(d)} + b, \]

where the geometric factors are \( a = \frac{1}{2} (1 - m_n) \), \( d_1 = \lambda_1 (1 - m_n) \), \( d_2 = \lambda_2 (1 - m_n) \), and \( d_3 = 1 - m_n \); the constant factors are \( b = m_1 D_i \),

\[ c_i = \frac{1}{2} m_1 (1 - m_n) \left( s_i^{(0)} - s_i^{(d)} \right), \]

for \( i = 1, 2, \) and

\[ a_0 = m_1 (1 - m_n) m_2 (p_i^{(d)} - p_i^{(0)}) \left( s_i^{(0)} - s_i^{(d)} \right), \]

where \( \lambda_1 \) and \( \lambda_2 \) are the eigenvalues in (C1) and \( \lambda_1 \) and \( \lambda_2 \) are the coefficients in (C5). Iterating the \( D_i \) recursion shows that in any generation \( t \).
\[ D_j^{(0)} = \left( D_j^{(0)} - \sum_{k=1}^{3} \frac{c_k}{a_k} - D_0 \right) a' \]

\[ = \sum_{k=1}^{3} \frac{c_k}{a_k} + D_0 \quad (C6) \]

provided that \( \lambda_0 = 1/\alpha \), while if \( \lambda_0 = 1/\beta \), then

\[ D_j^{(0)} = \left( D_j^{(0)} + \sum_{k=1}^{3} \frac{c_k}{a_k} - \sum_{k=1}^{3} \frac{c_k}{a_k} - D_0 \right) a' \]

\[ + \frac{\gamma_1}{a_1} + \frac{\gamma_2}{a_2} + D_0 \quad (C7) \]

In both solutions, (C6) and (C7), the dominant term is \( d_i = (1 - m_0)^i \) and

\[ D_j^{(0)} \rightarrow D_0 = \frac{3}{1 - m_0} = \frac{2mD_0}{1 - m_0} \quad \text{as} \quad i \rightarrow \infty. \]

**APPENDIX D**

**CENSUS 2 FOR HAPLOIDIOIDS: 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 \( z = mz + (1 - m)z_i \), where \( z_i \) is the corresponding value in the m and \( z \) is the corresponding sex-specific migration rate, while the interim value of \( z_i \) after migration is given by

\[ D_0 = mD_0 + (1 - m)D_0 + \frac{m}{(1 - m)} (\beta - \beta') (\alpha - \beta') \]

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

\[ w_i = 0, (\alpha + 1 - \alpha) P_i \]

\[ w_i = 0, (\beta + 1 - \beta) P_i \]

while those for the composite female cytonuclear genotypes are

\[ w_i = \beta P_i + \alpha \beta P_i \]

\[ w_i = \beta P_i + \alpha \beta P_i \]

\[ w_i = \beta P_i + \alpha \beta P_i \]

\[ w_i = \beta P_i + \alpha \beta P_i \]

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

\[ w_i' = \beta P_i + \alpha \beta P_i \]

\[ w_i' = \beta P_i + \alpha \beta P_i \]

\[ w_i' = \beta P_i + \alpha \beta P_i \]

\[ w_i' = \beta P_i + \alpha \beta P_i \]

while the new allele frequencies in females are

\[ p_i' = \beta P_i + \alpha \beta P_i + \alpha \beta P_i - \beta \beta P_i \]

\[ q_i' = \beta P_i \]

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

\[ D_1 = \beta P_i + \alpha \beta P_i \]

\[ D_1 = \alpha \beta P_i + \beta \beta P_i \]

\[ D_1 = \beta P_i - \beta \beta P_i \]

\[ D_1 = \beta P_i + \alpha \beta P_i + \beta \beta P_i \]

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

\[ (P_i') = \beta P_i \]

\[ (P_i')' = \beta P_i \]

\[ (P_i') = \beta P_i \]

\[ (P_i')' = \beta P_i \]

for \( i = 1, 2 \) for the genotype frequencies, and

\[ p_i' = \beta P_i \]

\[ q_i' = \beta P_i \]

\[ D_0' = D_0 \]

for the allele frequencies and disequilibria 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 (APENDIX A). The equilibrium frequencies of pure type individuals, \( \hat{\alpha}_0, \hat{\beta}_0, \hat{P}_0, \) and \( \hat{Q}_0, \) can be obtained directly from the census 1 values (APPENDIX B) and the intercensus relationship in (30). The time-dependent solution for the female cytonuclear frequency has the same form as that under census 1 in (22). Moreover, the male cytoype frequency now has this very same dynamics, since we see from (D3) and (D5) that under census 2, \( x_i' = x_i^{(0)} \) for all \( i \geq 1 \). The equilibrium nuclear allele frequencies in the two sexes are

\[ \hat{m}_P' = \frac{m_0 \hat{P}_0 + (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0}{2m_0 + (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0} \]

\[ \hat{m}_P' \times \frac{1 - (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0}{2m_0 + (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0} \]

and

\[ \hat{m}_P' + (1 - m_0) \hat{P}_0 \]

\[ \times \frac{1 - (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0}{2m_0 + (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0} \]

and

\[ m_0 \hat{P}_0 + (1 - m_0) \hat{P}_0 \]

\[ \times \frac{1 - (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0}{2m_0 + (1 - m_0) \hat{P}_0 + m_0 \hat{P}_0} \]
and the final disequilibria are

\[
D_B = \frac{m_D + a \bar{D}_B + \bar{m} \bar{D}_B}{1 + m_D}
\]

\[
D_B = \bar{m}_D + a \bar{D}_B + \bar{m} \bar{D}_B
\]

\[
D_B = (\bar{m}_D - \bar{m}_D) \bar{D}_B - a \bar{D}_B \bar{D}_B + \bar{m} \bar{D}_B \bar{D}_B
\]

\[
D_B = -\bar{m}_D \bar{D}_B - \bar{m}_B \bar{D}_B \bar{D}_B
\]

where, for any variable \( z \) on the right-hand side, including \( D_B \), \( z = \bar{z} + (1 - \bar{m}) z \), with \( m \) replaced by \( m \) for female variables or by \( m_B \) for male variables. Note that the equilibrium sign pattern \( D_B < 0 < D_B, D_B, D_B \) holds for census 2 whenever there is a positive allelic association in the migrant females (\( D_B > 0 \)). The equilibrium 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 (\( a = b = 0 \)), the time-dependent solutions for the variables \( p^{(+)} \), \( p^{(0)} \), and \( D^{(0)} \) are obtainable using the solutions for census 1 found in appendix C together with the intercensus relationship given in (29) for the frequencies and

\[
D^{(+)}(0) = m_D + (1 - m_B) D^{(+)}(1)
\]

\[
+ m_B (1 - m_B) (p^{(+)}(1) - p^{(+)}(0)) (x^{(+)}(1) - x^{(+)}(0))
\]

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

\[
\tilde{p}_B = \frac{m_B (2 - m_B) \tilde{p}_B + m_B \tilde{p}_B}{2m_B (1 - m_B) \tilde{p}_B}
\]

\[
\tilde{p}_B = \frac{m_B (2 - m_B) \tilde{p}_B + m_B \tilde{p}_B}{2m_B (1 - m_B) \tilde{p}_B}
\]

which, like census 1, are weighted averages of \( \tilde{p}_B \) and \( \tilde{p}_B \).

The steady-state disequilibria also simplify considerably, and the final male allelic disequilibrium is now simply twice the value in females,

\[
D_B = 2D_B = \frac{2m_D}{1 + m_D}
\]

with \( D_B \) now at most half the value in the migrant females (i.e., \( D_B \leq \frac{1}{2} D_B \)). Under census 2, the equilibrium sign pattern of \( D_B \) and \( D_B \) having the same sign, and \( D_B \) the opposite sign of \( D_B \) 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** (\( 0 < m_B < 1, m = 0 \)). 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., \( x^{(+)} = x^{(0)} \)) and thus all male equilibria equal those in females (\( z = \bar{z} \)). 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 the two qualitative distinctions of censuses 2 for male migration only are that the cytotype frequencies in both sexes will always equal the initial value in females (\( x^{(+)} = x^{(0)} = x^{(0)} \) for all \( t = 1 \) and all cytonuclear disequilibria (including \( D_B \)) will ultimately decay to zero.

**Female migration only** (\( 0 < m_B < 1, m = 0 \)). 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 \( x_B \)) 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 SLIP-KNIFE MODEL FOR CENSUS 1**

From the recessives given in (15) and (32), it can be shown that \( \tilde{u}_k \), must satisfy the quadratic equation

\[
f(u_k) = A_k u_k + B_k u_k + C_k = 0 \quad (E_1)
\]

where

\[
A_k = (1 - \alpha) (1 - m_B)
\]

\[
B_k = \alpha (1 - m_B) + (1 - \alpha) (1 - m_B) m_B u_k
\]

\[
- (1 - \alpha) m_B (1 - m_B) u_k - 1
\]

\[
C_k = m_B u_k
\]

with the corresponding male equilibrium given by

\[
\tilde{p}_B = \frac{\alpha (1 - m_B) u_k + m_B \tilde{p}_B}{1 - (1 - \alpha) (1 - m_B) u_k}
\]

The expression of the sign of the quadratic (E1) at \( u_k = 0 \), \( u_k = 1 \), and as \( u_k \to \infty \) shows that when \( 0 < m_B, u_k < 1 \) and \( 0 < a, m_B, \tilde{p}_B < 1 \), there is a single, admissible equilibrium solution in \( 0 < u_k \) for \( u_k \), and \( \tilde{p}_B \) correspond to the smaller root of \( (E_1) \). Also, since

\[
f(u_k) = - (1 - \alpha) (1 - m_B)
\]

\[
\times (1 - m_B \tilde{p}_B - (1 - m_B) u_k) u_k < 0
\]

and, on \( (0, 1) \), \( f(u_k) < 0 \) if and only if \( u_k < u_k < 1 \),
then $\alpha_i < \beta_i$. For males, however, $\beta_i^* \geq \gamma_i^*$ if $\beta_i^* < \gamma_i$ and

$$\alpha > \frac{\beta_i^* [1 - m_i \beta_i - (1 - m_i) \gamma_i^*]}{(1 - \beta_i) [m_i \beta_i + (1 - m_i) \beta_i^*]}.$$  

Analogous formulas and results hold for the pure species 2 individuals with $u_i$, replaced by $u_i$, $v_i$ by $v_i$, $p_i^*$ by $p_i^*$, $\beta_i^*$ by $\gamma_i$, and $\alpha$ by $\beta$.

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 $f_i(x)$ and $\bar{g}_i(x)$, corresponding to the two pure species, since only the recursions of the pure parental males have changed under the X-linked model. Expanding out $f_i(x)$ for the X-linked case reveals that its roots are $\lambda_0 = 0$ and

$$\lambda_i = \alpha (1 - m_i) + (1 - \alpha) \times [(1 - m_i)^{\beta_i^*} + (1 - m_i) \beta_i^*]$$

obtained from (15) and (32). into (ES), we find that $0 < \lambda_i < 1$ if and only if $\beta_i^* < -\beta_i^{\gamma_i}/(5m_i)$, where, as in the haplodiploid case, this fraction is the critical point of the quadratic defining $\beta_i$, given in (E1). Since $\beta_i^*$ is the smaller root, this inequality must hold. By symmetry, the roots of $\bar{g}_i(x)$ 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.