Dynamics of Gene Differentiation Between Incompletely Isolated Populations of Unequal Sizes

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The progress of gene differentiation between two populations of unequal sizes is studied by taking into account the effects of mutation and migration. Explicit formulae for the eventual rate of approach to equilibrium of the probabilities of identity of genes by descent within and between populations are worked out for the case of small migration. Formulae for the equilibrium values of identity probabilities are also given for some special cases. It is shown that in the case of large migration the Nei–Feldman formulae for the temporal changes and equilibrium values of identity probabilities approximately hold, unless the sizes of the two populations are extremely different. The theories developed are applied to study the evolution of cave fish populations in Astyanax mexicanus. The approximate time after divergence between the cave and river populations of this fish has been estimated to be 525,000–710,000 years, which agrees well with the geological data on cave formation.

INTRODUCTION

Nei and Feldman (1972) studied the dynamics of gene differentiation between two incompletely isolated populations in terms of the probabilities of identity of genes by descent within and between populations. Taking into account the effects of mutation, migration and genetic random drift, they developed a general formula by which the identity probabilities and genetic distance between populations can be obtained for any generation. Latter (1973) also studied the gene differentiation among a number of populations by using a modified island model. These studies are based on the assumption of an equal size of all populations. This assumption, however, often fails to hold in nature, and thus the applicability of the theories developed is restricted.

The primary purpose of this paper is to remove this assumption and study the gene differentiation between populations of unequal sizes. Removal of the assumption makes it difficult to obtain an explicit general formula, but it is

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possible to study some important cases by an analytical method. We shall use Nei and Feldman's model because of its simplicity and practical interest. The results obtained will be applied to the gene frequency data from the characid fish *Astyanax mexicanus* to study the evolution of cave fish.

**Mathematical Formulation**

Suppose that a population splits into two incompletely isolated populations and thereafter gene migration occurs in every generation between the two populations with a constant rate. Let $N_1$ and $N_2$ be the sizes of populations 1 and 2, respectively, and assume that they remain constant for all generations. We also assume that the effective size is the same as the actual size. If the two populations exchange $M$ individuals per generation, the rate of migration in populations 1 and 2 are given by $m_1 = M/N_1$ and $m_2 = M/N_2$, respectively. In some cases, however, this simple relationship may not hold. For example, if one of the two populations inhabits an adverse environment, the number of immigrants into this population may be larger than the number of emigrants but still a constant size may be maintained because of a low viability. In an extreme case only unidirectional migration may occur. To cover these situations, we use the migration rates defined as $m_1 = M_1/N_1$ and $m_2 = M_2/N_2$, where $M_1$ and $M_2$ are the numbers of immigrants per generation in populations 1 and 2, respectively. Theoretically, $m_1$ and $m_2$ can take any value between 0 and 1, but we confine our discussion to the case of $m_1 + m_2 \ll 1$, since the sum of the two migration rates would never be larger than unity in nature. Note that $m_1 = m_2 = 0.5$ with $N_1 = N_2$ corresponds to the case of random mating in the whole population. We further assume that each new mutation is different from the alleles preexisting in any of the two populations. No selection will be considered in the present paper.

Let $J_{11}^{(t)}$ and $J_{22}^{(t)}$ be the probabilities of identity of two randomly chosen genes from populations 1 and 2, respectively, at generation $t$. In randomly mating diploid populations these quantities measure the average homozygosity. We denote by $J_{12}^{(t)}$ the probability of identity of two randomly chosen genes, one from each of the two populations. The temporal change of this quantity is of great interest, since the number of codon differences per locus between the two populations basically depends on this value (Nei, 1972).

Following Malécot (1969), we can derive the recurrence equations for $J_{11}^{(t)}$, $J_{12}^{(t)}$ and $J_{22}^{(t)}$. They become

\[
J_{11}^{(t+1)} = (1 - u)^2 \left[ \left( 1 - m_1 \right)^2 \left\{ \frac{1}{2N_1} + \left( 1 - \frac{1}{2N_1} \right) J_{11}^{(t)} \right\} \right.
\]

\[
+ 2m_1 (1 - m_1) J_{12}^{(t)} + m_1^2 \left\{ \frac{1}{2N_2} + \left( 1 - \frac{1}{2N_2} \right) J_{22}^{(t)} \right\} \right],
\]

(1a)
\[ j_{12}^{(\ell+1)} = (1 - u)^2 \left[ m_2(1 - m_1) \left\{ \frac{1}{2N_1} + \left(1 - \frac{1}{2N_1} \right) j_{11}^{(\ell)} \right\} \right. \\
+ (m_1 m_2 + (1 - m_1)(1 - m_2)) j_{12}^{(\ell)} \\
+ m_2(1 - m_2) \left\{ \frac{1}{2N_2} + \left(1 - \frac{1}{2N_2} \right) j_{22}^{(\ell)} \right\} \]. \\
(1b)

\[ j_{22}^{(\ell+1)} = (1 - u)^2 \left[ m_2 \left\{ \frac{1}{2N_1} + \left(1 - \frac{1}{2N_1} \right) j_{11}^{(\ell)} \right\} \\
+ 2 m_2(1 - m_2) j_{12}^{(\ell)} \\
+ (1 - m_2)^2 \left\{ \frac{1}{2N_2} + \left(1 - \frac{1}{2N_2} \right) j_{22}^{(\ell)} \right\} \right]. \\
(1c)

When \( N_1 = N_2 \) and \( m_1 = m_2 \), the above equations reduce to those of Nei and Feldman (1972).

The Eqs. (1a), (1b), and (1c) may be expressed in the following way by using the matrix notation.

\[ J^{(\ell+1)} = (1 - u)^2 T + (1 - u)^2 \mathbf{M} J^{(\ell)}, \]

where

\[ J^{(\ell')} = (j_{11}^{(\ell)}, j_{12}^{(\ell)}, j_{22}^{(\ell)}), \]

\[ T' = \left( \frac{(1 - m_1)^2}{2N_1}, \frac{m_1^2(1 - m_1)}{2N_1}, \frac{m_1(1 - m_1)}{2N_1}, \frac{m_2(1 - m_2)}{2N_2}, \frac{m_2^2}{2N_2}, \frac{(1 - m_2)^2}{2N_2} \right), \]

and

\[ \mathbf{M} = \begin{bmatrix}
(1 - m_1)^2(1 - \frac{1}{2N_1}) & 2m_1(1 - m_1) & m_1^2\left(1 - \frac{1}{2N_1}\right) \\

m_2(1 - m_1)\left(1 - \frac{1}{2N_1}\right) & 1 - m_1 - m_2 + 2m_1m_2 & m_2(1 - m_2)\left(1 - \frac{1}{2N_2}\right) \\
m_2^2\left(1 - \frac{1}{2N_1}\right) & 2m_2(1 - m_2) & (1 - m_2)^2\left(1 - \frac{1}{2N_2}\right)
\end{bmatrix}. \]

The evolutionary change of \( J \) is determined by the eigenvalues and eigenvectors of \( \mathbf{M} \). There are three eigenvalues, \( \lambda_1, \lambda_2, \) and \( \lambda_3 \), for which the general solutions are not easy to obtain. However, it can be shown that \( 0 < \lambda_1, \lambda_2, \lambda_3 < 1 \).

The vector of equilibrium identity probabilities, \( J^{(\infty)} \), is given by

\[ J^{(\infty)} = (1 - u)^2 (\mathbf{I} - (1 - u)^2 \mathbf{M}^{-1}) T. \]

(3)
GENE DIFFERENTIATION

EQUILIBRIUM IDENTITY PROBABILITIES

Studying the equilibrium identity probabilities, Nei and Feldman (1972) concluded that the gene differentiation between populations becomes appreciable only when the migration rate is extremely small. Let us first study this problem, since this reveals which cases should be studied in detail. The equilibrium values of identity probabilities can be studied numerically by using (3).

The degree of gene differentiation between populations may be measured by the normalized identity of genes, which is expressed as $I = \frac{J_{12}}{(J_{11}J_{22})^{1/2}}$ (Nei, 1972). Table I shows the values of this quantity for different migration rates and population sizes. ($N_2$ denotes the size of the smaller population.) In the computation of these values $m_1N_1 = m_2N_2$ (balanced migration) and $u = 10^{-5}$ were assumed. It is seen that the $I$ value is small when $m_1 + m_2$ is small and the difference between $N_1$ and $N_2$ is large, as expected. However, $I$ is close to 1 if $m_1 + m_2 > 10^{-2}$ and the ratio $N_1/N_2$ is less than 10 with $N_2 > 100$. In nature, even a small population would be generally larger than 100. So, we may conclude that the gene differentiation between two populations becomes appreciable only when migration rate is very small, even if the sizes of the two populations are considerably different. This indicates that the study of temporal changes of identity probabilities is meaningful only when the migration rate is very small. Fortunately, this is the case in which approximate eigenvalues of $M$ can be obtained.

The above conclusion holds true even if migration is unidirectional. This will be discussed in the next section in conjunction with the temporal changes of identity probabilities, since in this case a simple analytical expression for $J^{(\infty)}$ is obtainable.

<table>
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<tr>
<th>$N_2$</th>
<th>$m_1 + m_2$</th>
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<td>.0476</td>
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<td></td>
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<td>.9701</td>
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<td></td>
<td>$10^{-2}$</td>
<td>.9980</td>
<td>.9949</td>
<td>.9616</td>
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The results obtained above suggest that the Nei–Feldman formula, which is based on the assumption of equal population size, may hold sufficiently accurately even if the actual sizes are considerably different. If this is so, it has a great practical utility. Thus, the equilibrium values \((J^{(q)}_{ij})\) of identity probabilities when \(N_1 \neq N_2\) were compared with those \((J^{(q)}_{ij})\) of the case where the sizes of the two populations are assumed to be equal to the arithmetic mean of \(N_1\) and \(N_2\). In this computation again balanced migration and \(u = 10^{-6}\) were assumed. Table II shows the differences between these two equilibrium values.

**TABLE II**

Comparisons of the Identity Probabilities \((J^{(q)}_{ij})\) when \(N_1 \neq N_2\) with those \((J^{(q)}_{ij})\) when the Sizes of the Two Populations Are Assumed to Be Equal to the Arithmetic Mean of \(N_1\) and \(N_2\). \(d_{ij} = J^{(q)}_{ij} - J^{(q)}_{ij}\)

<table>
<thead>
<tr>
<th>(m_1 + m_2)</th>
<th>(N_1/N_2)</th>
<th>(d_{11})</th>
<th>(d_{12})</th>
<th>(d_{22})</th>
</tr>
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<td>.0002</td>
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</tr>
<tr>
<td></td>
<td>100</td>
<td>.0034</td>
<td>.0014</td>
<td>-.1976</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>.0016</td>
<td>.0011</td>
<td>-.5667</td>
</tr>
<tr>
<td>0.01</td>
<td>10</td>
<td>(6.7 \times 10^{-4})</td>
<td>(7.0 \times 10^{-4})</td>
<td>-.0067</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>(5.9 \times 10^{-4})</td>
<td>(3.9 \times 10^{-4})</td>
<td>-.0555</td>
</tr>
<tr>
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<td>1000</td>
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<td>(3.1 \times 10^{-4})</td>
<td>-.1576</td>
</tr>
<tr>
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<td>-.0007</td>
</tr>
<tr>
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<td>-.0059</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>(1.7 \times 10^{-5})</td>
<td>(3.2 \times 10^{-7})</td>
<td>-.0167</td>
</tr>
</tbody>
</table>

\((d_{ij} = J^{(q)}_{ij} - J^{(q)}_{ij})\) for various population sizes and migration rates. It is clear that if \(m_1 + m_2\) is larger than 0.01, \(d_{ij}\) is small, even if \(N_1\) and \(N_2\) are considerably different. When \(m_1 + m_2\) is small, \(d_{22}\) can be large if \(N_1/N_2\) is large, but \(d_{11}\) and \(d_{12}\) remain to be small. Therefore, as long as \(m_1 + m_2\) is large, the Nei–Feldman formula for equilibrium identity probabilities may be used even for the case of unequal population sizes.

The temporal changes of identity probabilities were also studied numerically. It was shown that the Nei–Feldman formula holds true approximately in this case, too.

**TEMPORAL CHANGES OF J\(^{(q)}\) IN SOME SPECIAL CASES**

Let us now consider the temporal change of \(J^{(q)}\) in some special cases. We shall confine ourselves to the following three cases, since other cases can be studied approximately by the Nei–Feldman formula, unless the sizes of the two populations are extremely different.
1. Complete Isolation \( (m_1 = m_2 = 0) \)

This case is mathematically rather trivial but biologically important. Clearly, we have \( J_{11}^{(0)} = J_{11}^{(0^*1)} + (J_{11}^{(0)} - J_{11}^{(0^*)})((1 - u)^2(1 - 1/2N_1)^2) \) for \( i = 1, 2 \), and \( J_{12}^{0} = J_{12}^{(0)}(1 - u)^{2u} \), where \( J_{11}^{(0)} = 1/(4N_1u + 1) \) approximately.

In the evolutionary process a small group of individuals is often derived from a large population and undergoes separate evolution. In this case the identity of genes in the large population \( (J_{11}^{(0)}) \) may remain constant, while that in the small population \( (J_{12}^{0}) \) may change considerably because of a reduced population size. The normalized identity of genes, \( I^{(0)} = J_{12}^{(0)^2}/(J_{11}^{(0)} J_{12}^{(0)})^{1/2} \), will then be related to the evolutionary time in a complicated way. However, if \( J_{12}^{(0)} = J_{11}^{(0)} = J_{12}^{(0)^*} \),

\[
I^{(0)} = J_{12}^{(0)^2}/J_{11}^{(0)} \approx e^{-2ut}. \tag{4}
\]

Therefore, \( I^{(0)} \) declines exponentially as \( t \) increases. We shall use this formula to estimate the evolutionary time of cave fish populations.

2. Small Migration Rates \( (m_1, m_2 \ll 1) \)

If migration rates are very small and the second order terms of \( m_1 \) and \( m_2 \) can be neglected, the eigenvalues of \( M \) are approximately given by \( \lambda_1 = 1 - 2m_1 - 1/(2N_1) \), \( \lambda_2 = 1 - m_1 - m_2 \), and \( \lambda_3 = 1 - 2m_2 - 1/(2N_2) \). If \( N_1 > N_2 \) and \( m_2 - m_1 > 1/(2N_1) \), then \( \lambda_1 \) becomes the dominant eigenvalue and the eventual rate of approach to equilibrium is given by \( 1 - \lambda_1(1 - u)^2 \approx 2(u + m_1) + 1/(2N_1) \). On the other hand, if \( N_1 > N_2 \) and \( m_2 - m_1 < 1/(2N_1) \), \( \lambda_2 = 1 - m_1 - m_2 \) is the dominant eigenvalue and the eventual rate of approach to equilibrium is given by \( 2u + m_1 + m_2 \) approximately.

It can be shown that the equilibrium identity probabilities are given by

\[
J_{1i}^{(0)} = (1 - 2m_1 - 2u)(4N_i(u + m_i) + 1)^{-1} \quad \text{for } i = 1, 2, \tag{5a}
\]

\[
J_{11}^{(0)} = (1 - 2u)m_2/(2N_1) + m_1/(2N_2). \tag{5b}
\]

approximately. The normalized identity of genes is

\[
I = (m_1 + m_2)/(m_1 + m_2 + 2u) \tag{6}
\]

approximately, if \( u \ll m_1, m_2 \ll 1 \). Thus, the genetic distance between the two populations is \( D \approx 2u(m_1 + m_2) \). This indicates that an appreciable extent of gene differentiation occurs only when migration rates are very small. When \( m_1 = m_2 \), (6) reduces to the formula given by Nei and Feldman (1972).

3. Unidirectional Migration \( (m_2 \neq 0, m_1 = 0) \)

We assume that migration occurs only from population 1 to population 2. The eigenvalues of \( M \) are given by \( \lambda_1 = 1 - 1/(2N_1) \), \( \lambda_2 = 1 - m_2 \), and
\[ \lambda_2 = (1 - m_2)^2 \left( 1 - \frac{1}{2N_2} \right) \]. Therefore, if \( m_2 > 1/(2N_2) \), \( \lambda_2 \) is the dominant eigenvalue, whereas if \( m_2 < 1/(2N_2) \), \( \lambda_2 \) is the dominant eigenvalue.

Clearly, \( J_{11}^{(m)} = (4N_1c + 1)^{-1} \), where \( c = \left[ 1 - (1 - u)^2 \right]/\left[ 2(1 - u)^2 \right] \), while

\[
\begin{align*}
J_{12}^{(m)} &= \frac{m_2}{1 - (1 - m_2)(1 - u)^2} \left( 4N_1c + 1 \right)^{-1}, \\
J_{21}^{(m)} &= (1 - u)^2 \left[ x \left\{ \frac{(1 - m_2)^2}{2N_2} + \frac{m_2^2}{2N_1} \right\} + \frac{m_2}{2N_1} y + \frac{z}{2N_1} \right],
\end{align*}
\]

where

\[
x = \frac{1}{1 - (1 - u)^2} \left\{ 1 - m_2 \right\}^{2} \left( 1 - \frac{1}{2N_2} \right),
\]

\[
y = \frac{2m_2(1 - m_2)(1 - u)^2}{\left[ 1 - (1 - m_2)(1 - u)^2 \right] \left[ 1 - (1 - u)^2 \right] \left[ 1 - (1 - m_2)(1 - u)^2 \right]},
\]

\[
z = \frac{m_2^2(1 - u)^2(1 - 1/2N_2)(1 + (1 - m_2)(1 - u)^2)}{\left[ 1 - (1 - u)^2 \right] \left[ 1 - m_2 \right] \left[ 1 - (1 - u)^2 \right] \left[ 1 - (1 - m_2)(1 - u)^2 \right] \left[ 1 - (1 - u)^2 \right] \left[ 1 - (1 - m_2)(1 - u)^2 \right]}.
\]

If \( u \ll m_2 \ll 1 \), \( J_{11}^{(m)} \), \( J_{12}^{(m)} \), and \( J_{22}^{(m)} \) reduce to

\[
(4N_1u + 1)^{-1}, \quad m_2/(2u + m_2)(4N_1u + 1)], \quad \text{and} \quad [4N_1(u + m_2 + 1)^{-1},
\]

respectively. Thus, \( I \approx m_2/(m_2 + 2u) \). The effect of migration from population 2 to population 1 can be studied similarly by interchanging the subscripts in the above formulae.

Figures 1 and 2 show the equilibrium values of \( J_{11} \), \( J_{12} \), and \( J_{22} \) for the cases of unidirectional migration from population 1 (\( m_1 = 0; m_2 \neq 0 \)) and from population 2 (\( m_1 \neq 0; m_2 = 0 \)), respectively. In both cases \( u = 10^{-5} \), \( N_1 = 10,000 \), and \( N_2 = 100 \) were assumed. In the first case \( J_{11} \) remains constant, since no immigrant enters into population 1. \( J_{22} \) is large when \( m_2 \) is of the order

![Identity Probability](image_url)

**Fig. 1.** Steady-state identity probabilities within \((J_{11}, J_{12})\) and between \((J_{12})\) populations under unidirectional migration \((m_1 = 0, m_2 \neq 0)\).
of mutation rate, but decreases gradually as $m_2$ increases and becomes almost equal to $J_{11}$ when $m_0 = 0.1$. On the other hand, $J_{12}$ is small when $m_0$ is small, as expected, but this quantity increases rather quickly as $m_0$ increases and reaches the same level as that of $J_{12}$ at around $m_0 = 10^{-3}$. In the case of unidirectional migration from population 2 to population 1, $J_{21}$ remains constant. As $m_1$ increases from 0, $J_{11}$ first decreases slightly and then rapidly increases to reach the level of $J_{22}$ around $m_1 = 0.001$. The initial decrease of $J_{11}$ is caused by the fact that a small amount of migration has the same effect as that of mutation. If $m_1$ is large, however, $J_{11}$ increases, because the immigrants are highly inbred in this case. The increase of $J_{12}$ from 0 to the level of $J_{22}$ is also explained by the same reason.

**Examples from the Evolution of Cave Fish**

Avise and Selander (1972) studied the gene frequencies for 17 protein loci in three cave and six river populations of the characid fish *Astyanax mexicanus* in Mexico. One of the cave populations studied, i.e., Pachón, appears to be almost entirely isolated from the river populations, and the fish in this cave are uniformly eyeless and unpigmented. The fish in another cave, Los Sabinos, are also uniformly eyeless and unpigmented, but there is a possibility that migration occurs between this cave and its neighboring river populations at the time of flooding after heavy rain. The third cave (Chica) contains fish showing the full range of variation from eyeless and unpigmented to fully eyed and darkly pigmented, and there is evidence that migration occurs between this cave and its neighboring river populations (Avise and Selander, 1972). The size of these
cave populations has been estimated to be 200 to 500, while the size of river populations is not known but very large. In this paper we shall consider the evolution of the first two cave populations to illustrate the application of the theory developed.

If \( x_{ij} \) and \( y_{ij} \) are the frequencies of the \( j \)th allele at the \( i \)th locus in populations 1 and 2, then the identity probabilities are computed by

\[
J_{11} = \sum_{ij} x_{ij}^2 / n, \quad J_{12} = \sum_{ij} x_{ij} y_{ij} / n, \quad J_{22} = \sum_{ij} y_{ij}^2 / n,
\]

where \( n \) is the total number of loci studied (Nei, 1972). The values of these quantities and their standard errors (Nei and Roychoudhury, 1974a) for the two cave populations and their respective neighboring river populations (Arroyo B and Arroyo Valles) are given in Table III. It is seen that the homozygosities of

<table>
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<th>Surface Populations</th>
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<td>Pachon</td>
<td>Los Sabinos</td>
</tr>
<tr>
<td>Pachon</td>
<td>1.000 ± 0.0</td>
<td>.798 ± .095</td>
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<tr>
<td>Los Sabinos</td>
<td>.964 ± .030</td>
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<td>Arroyo Valles</td>
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<td>.867 ± .044</td>
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the two cave populations are both very high, as expected from their small population sizes. On the other hand, the two river populations are highly heterozygous and share a large fraction of common genes, the normalized identity of genes the two populations (I) being 0.995. The identity probabilities between the cave and river populations indicate that a substantial gene differentiation has occurred between these populations.

Let us now study the evolutionary change of the cave populations, assuming that gene differentiation occurs mainly by mutation and genetic random drift. We note that in small populations such as the present cave fish genetic random drift plays an important role. A rough estimate of the evolutionary time can then be obtained by (4), assuming no migration. We assume that the ancestral populations of the Pachon and Los Sabinos fish are their nearby river populations Arroyo B and Arroyo Valles, respectively, and that the average homozygosities \( J_{22}^{(o)} \) of each cave population when it was formed was the same as the present level of homozygosity in its ancestral population. Then, the \( J_2^{(i)} \) value is
0.7788/0.8978 = 0.8675 for the Pachon cave and 0.9008 for the Los Sabinos. Thus, the genetic distance, \( D = -\log_n I_i^{(t)} = 2ut_i \), is 0.142 ± 0.092 for the former and 0.105 ± 0.066 for the latter. It is interesting to note that these values of genetic distance are the same order of magnitude as that of the semispecies in mice (Nei, 1972). From amino acid substitution data for some proteins, Kimura and Ohta (1971) and Nei and Roychoudhury (1974b) have estimated that \( u \) is roughly 10^{-7} per locus per year for electrophoretically detectable proteins. The estimate of evolutionary time, therefore, becomes 710,000 ± 460,000 years for the Pachon population and 525,000 ± 330,000 years for the Los Sabinos population. Interestingly, these estimates agree well with the geological estimate of the time of formation of caves in this region of Mexico (the Pleistocene).

As mentioned earlier, there is the possibility that a small rate of migration occurs from rivers to the Los Sabinos population. A slightly lower estimate of evolutionary time for this population than for the Pachon may be due to this migration. A maximum estimate of the migration rate may be obtained by assuming that the population has reached the steady state with mutation, migration and genetic random drift. In this case migration must be unidirectional from the river to the cave population. At the steady state, therefore, we have \( m_0 = (m_0 + 2u) \approx 0.901 \). This fish becomes sexually matured at the age of 6–8 months and remains fertile for about 15 years (P. Sadoglu, personal communication). If we assume that the generation time for this fish is 6 years and genetic drift is much more important than selection, the mutation rate per generation (\( u \)) is estimated to be \( 6 \times 10^{-7} \) per generation. Then, a maximum estimate of migration rate is \( 1.09 \times 10^{-6} \) per generation. This indicates that the migration rate is only slightly higher than the mutation rate, if it really occurs.

References


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