Effect of Changing Partnership Formation Rates on the Spread of Sexually Transmitted Diseases and Human Immunodeficiency Virus

Hein Stigum, Per Magnus, and Leiv S. Bakketeig

Core population groups play an important role in the spread of sexually transmitted diseases. Subjects in a core group may change their behavior over time and “migrate” to the noncore. The authors examined the effects of such migration on the prevalence of gonorrhea, chlamydia, and human immunodeficiency virus (HIV) using a mathematical model. The size of the core and the migration rate from the core to the noncore were estimated from population-based sexual survey data on 8,445 Norwegians collected in 1987 and 1992. Sixty-four percent of the sample was considered without risk of contracting a sexually transmitted disease. The core group made up 2.5% of the remaining sample. The migration rate from the core was estimated at 12% per year. The three types of infections analyzed exemplify three different patterns of the effect of migration on infection prevalence in the core/noncore groups: gonorrhea = no effect/no effect, chlamydia = no effect/increase, and HIV = decrease/increase. Migration affects the basic reproductive ratio of diseases with a long infectious period more than that of diseases with a short infectious period. For HIV, this means that the later stages of infection contribute less to the basic reproductive ratio in the presence of migration. The results are qualitative and show that detailed knowledge about mixing, migration, transmission rates, and duration of infectiousness is necessary to make accurate predictions. Am J Epidemiol 1997;145:644-52.

HIV; models, statistical; sex behavior; sexual partners; sexually transmitted diseases

Editor's note: A companion article by Stigum et al. appears on page 636 of this issue.

Population subgroups with high levels of sexual activity are usually referred to as “core groups,” and they play an important role in the spread of sexually transmitted diseases (STDs) (1–4). In an accompanying paper (5), the frequency of sexual partner change among Norwegians was analyzed. One of the main findings was that people change their partner frequency over the course of a lifetime, mostly towards lower values. In this paper, we analyze how these changes affect STD levels and basic reproductive ratios in the core and noncore groups. Specifically, the rate of migration, defined as the proportion of persons who leave the core group per year due to a decrease in partner frequency, is estimated. In addition, the effects of migration on the prevalence of STDs in the core and noncore groups are studied, and the basic reproductive ratio for each STD both with and without migration is calculated. For human immunodeficiency virus (HIV), the contribution of each stage of infectiousness to the total reproductive ratio is calculated with and without migration. The analyses are based on data from two Norwegian sexual surveys conducted in 1987 and 1992 (5), using a mathematical model for the spread of STDs.

MATERIALS AND METHODS
Mathematical model

We examined the effects of migration from the core group to the noncore group on the prevalence of gonorrhea, chlamydia, and HIV using a mathematical model. The equations are given in the Appendix. The model is an extension of work presented previously (4). The STDs are characterized in terms of the transmission rate per sexual contact and the duration of infectiousness. Subjects with HIV infection progress through four stages: primary infection, asymptomatic infection, symptomatic infection, and acquired immunodeficiency syndrome (AIDS); each stage has a different duration and infectiousness. Sexual behavior is
described by partner and intercourse frequencies in each group, by the mixing between groups, and by the migration from the core. Subjects with five or more new partners per year are defined as belonging to the core group. Core group members change their behavior—that is, migrate to the noncore—at a constant rate. The migration rate is the same for infected subjects as for uninfected subjects. Migrants are replaced by uninfected subjects from the noncore, so that both groups remain the same size. The number of sexual contacts in the three types of partnerships (core/core, "mixed," and noncore/noncore) is also modeled. The mixed partnerships are assumed to be casual and short-lasting. The size of the core, the migration rate, and the mean partner and intercourse frequencies were estimated from the survey data. From the model, we calculated two output measures—the basic reproductive ratio and the number of infected subjects at equilibrium—with and without migration. The basic reproductive ratio, $R_0$, is the number of secondary cases produced by an average infected person over the period of infectiousness in a susceptible population. An epidemic can spread in a population if $R_0 > 1$. The calculations were done numerically in Mathematica (6). Many previously published articles have demonstrated an effect of partner mixing on STD spread (2, 3). The partner mixing pattern could not be estimated from our data. We therefore show the effects on migration in the case where partner mixing ranges from no mixing to proportional mixing. The basic reproductive ratio estimates are shown under the assumption of no partner mixing. For this situation, we can apply the analytic results given in equations 11–14 (Appendix). The model is fairly simple, and the emphasis is on qualitative rather than predictive results.

STD parameters

The transmission rates per episode of sexual intercourse and the durations of infectiousness are given in table 1. The values for gonorrhea and chlamydia were based on estimates published by Brunham and Plummer (7), with the transmission rates recalculated on a per-act basis. The recalculations were carried out according to the formula $\beta = 1 - (1 - \beta_p)^{1/\theta}$, where $\beta$ and $\beta_p$ are the transmission rates per contact and per partner, respectively, assuming that $\theta = 2$ contacts per partner. For HIV, the duration of each stage of infection and the transmission rates in stages 3 and 4 were based on estimates from Longini et al. (8). The transmission rate in stage 2 was based on the work of Jacquez et al. (9), and that in stage 1 was based on the work of Satten et al. (10) and Kunanusont et al. (11), modeling the possibly less infective serotype B, subtype B. The infectivity of core group members for HIV was assumed to be twice the values given in table 1 ($c_1 = 2$ and $c_2 = 1$ for HIV; see Appendix). A higher transmission rate for core members is likely if other STDs acting as cofactors for HIV transmission are more prevalent in the core. Results for HIV are shown for situations in which subjects with AIDS do and do not infect others, referred to as HIV stages 1–4 and HIV stages 1–3, respectively.

The model population was arbitrarily set to 10,000 individuals.

Sexual behavior surveys

Parameter estimation was based on data collected from 8,477 exclusively heterosexual Norwegians aged 18–52 years in two surveys of sexual behavior (5). Estimation of the migration rate was based on the 7,248 subjects from this sample for whom earlier partner frequency could be defined. Of the 8,477 subjects, 5,397 were married or cohabiting without extra partners. These subjects were considered without STD risk and were excluded from the estimation of the other parameters. Twenty subjects had missing data on cohabitation status or extra partners. The size of the core and the partner and unprotected intercourse frequencies were thus estimated from the remaining 3,060 subjects with potential STD risk behavior.

<table>
<thead>
<tr>
<th>TABLE 1. Estimates of transmission rate and duration of infectiousness for three sexually transmitted diseases*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Agent</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>-----------</td>
</tr>
<tr>
<td>Gonorrhea</td>
</tr>
<tr>
<td>Chlamydia</td>
</tr>
<tr>
<td>HIV†</td>
</tr>
</tbody>
</table>

* Based on previously published data (7–11).
† Persons with human immunodeficiency virus (HIV) infection progress through four stages: primary infection, asymptomatic infection, symptomatic infection, and acquired immunodeficiency syndrome.
‡ Doubled in the core group.
Variables

Recent partner frequency was defined as the number of new partners per year in the three most recent years before the survey. Earlier partner frequency was defined as the number of new partners per year during the period from age 16 to the three most recent years before the survey (5). Time under risk of migration was measured over the same period. Unprotected intercourse frequency was defined as the total number of sexual contacts per year in which a condom was not used (4). Subjects with a partner frequency of five or more belonged to the core group by definition.

The migration rate was defined as the proportion of subjects who left the core group per year due to a decrease in partner frequency to less than five new partners per year. It was assumed that the size of the core group was unchanged over time. If the size of the core group equals $n_c$ and the proportion of persons who migrate from the core per unit of time equals $\kappa$, then the cumulative number of migrants, $m$, at time $t$, equals

$$m(t) = n_c \kappa t.$$ (1)

To estimate the rate of migration from the survey data, we categorized subjects as belonging to the core or noncore group on the basis of both earlier and recent partner frequency. $n_c$ equals the number of subjects with a recent partner frequency $\geq 5$, and $m$ is the number of subjects with an earlier partner frequency $\geq 5$ but a recent partner frequency less than 5. $t$ is defined as the average period of time over which the earlier partner frequency is calculated for the $m$ group. The migration rate $\kappa$ can then be calculated from equation 1.

RESULTS

Behavior parameter values

The core group made up 2.5 percent of the 3,060 subjects with potential STD risk behavior. The estimated frequencies of partner change and unprotected intercourse were 7.6 and 109.6 per year, respectively, in the core group and 0.77 and 55.9 per year, respectively, in the noncore group. In accordance with the qualitative nature of the model, the frequencies of partner change and unprotected intercourse used were $\omega_1 = 8$, $\Psi_1 = 110$ per year, respectively, in the core group and $\omega_2 = 0.8$, $\Psi_2 = 55$ per year, respectively, in the noncore group. Note that partner frequency is 10 times as high in the core group as in the noncore group, whereas the intercourse frequency is only twice as high. This means that the average number of contacts per partner is much lower in the core than in the noncore.

A total of 127 subjects had been in the core group at some time but were not presently in the core group ($m$) (table 2). Their average period under risk of migration equaled 15.9 years ($t$). The present size of the core group equaled 66 subjects ($n_c$). Solving for $\kappa$ in equation 1 yielded an average migration rate $\kappa = 127/(66 \times 15.9) = 12$ percent per year. The number of contacts in a mixed partnership was assumed to be 1 ($\eta = 1$).

Effect of migration on STD spread

Below, we show the effects of migration on the basic reproductive ratio and on the numbers of persons infected at equilibrium for gonorrhea, chlamydia, and HIV. With 12 percent migration from the core group per year, infected subjects will move from the core to the noncore, thereby increasing the prevalence in the noncore and decreasing it in the core. The overall effect can be either an increase or a decrease in the total number of infected persons.

Effects on the basic reproductive ratio. The basic reproductive ratios under the assumption of no partner mixing are shown in table 3. With no migration, the core and the noncore are separate systems, each with their own $R_0$. All of the $R_0$'s are above 1 in the core and below 1 in the noncore, meaning that the infections

<table>
<thead>
<tr>
<th>TABLE 2. Earlier sexual partner* frequency according to recent partner† frequency among 7,248 heterosexual Norwegians aged 18–52 years, 1987 and 1992</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Recent partner frequency</strong></td>
</tr>
<tr>
<td>-----------------------------</td>
</tr>
<tr>
<td><strong>Earlier partner frequency</strong></td>
</tr>
<tr>
<td>2 ≤ 5</td>
</tr>
<tr>
<td>2 &gt; 5</td>
</tr>
<tr>
<td>Total</td>
</tr>
</tbody>
</table>

* From age 16 years to age 3 years prior to survey.
† Up to 3 years prior to survey.

<table>
<thead>
<tr>
<th>TABLE 3. Basic reproductive ratios ($R_0$) in the core and noncore groups when there is no migration from the core group, and in the core/noncore system when there is 12% migration from the core per year*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>0% migration</strong></td>
</tr>
<tr>
<td>Core</td>
</tr>
<tr>
<td>-----------------</td>
</tr>
<tr>
<td>Gonorrhea</td>
</tr>
<tr>
<td>Chlamydia</td>
</tr>
<tr>
<td>HIV stages 1–3</td>
</tr>
<tr>
<td>HIV stages 1–4</td>
</tr>
</tbody>
</table>

* Based on a mathematical model. Partner mixing is assumed to be zero.
† Percent decrease in the core basic reproductive ratio due to migration.
‡ HIV, human immunodeficiency virus.
can persist in the core but not in the noncore alone. With migration, the two groups form a system with one common \( R_0 \). When there is no partner mixing, its value is determined solely by the core group (equation 11). It therefore makes sense to compute the percentage difference in \( R_0 \) as in table 3. For infections with a short duration, such as gonorrhea, or a high \( R_0 \) without migration, such as chlamydia, the basic reproductive ratio is affected little by the migration. However, the \( R_0 \) for HIV changes a great deal in the presence of migration. Table 4 shows the contribution of each stage to the total \( R_0 \) for HIV stages 1–4. Migration affects the later stages more, and therefore the percentage contribution from each stage changes in the presence of migration, so that the short primary infection stage becomes even more important (see equation 11 in the Appendix).

Effects on the number of persons infected. The effects of migration on the number of infected subjects at equilibrium are shown in figures 1–4. Note that the scales in the right-hand panels differ between plots. The number of persons infected with gonorrhea is almost unaffected by migration (figure 1). For chlamydial infection, the core group is unaffected by the emigration, but immigration to the noncore leads to an increase in the number of infected subjects in that group. The increase is strongest for low partner mixing (figure 2). For HIV stages 1–3, migration leads to a strong decrease in the number of infected persons in the core; adding partner mixing can bring the prevalence to zero (figure 3). For HIV stages 1–4, migration leads to a strong decrease in the core but a strong increase in the noncore. At low partner mixing, the increase dominates, and an increase in the total number of infected persons due to migration is seen. At high partner mixing, the decrease dominates (figure 4). Here also, the combination of migration and partner mixing can bring the prevalence to zero.

The effects of migration alone—that is, in the absence of partner mixing—can be understood from equation 14 (Appendix). The equilibrium number of infected persons in the noncore group is given by the sum of two terms: the direct contribution of infected migrants and the number of secondary cases generated by these individuals. The latter figure contains the term total duration/(1 – \( R_0 \)), and it can be substantial if the basic reproductive ratio in the noncore (\( R_{02} \)) is close to 1, as for chlamydial infection, or the total duration of infectiousness is long, as for HIV.

With increasing mixing, more chains are begun in the noncore group, but these chains absorb some of the continuing chains that would otherwise have been sustained in the core group. At some point, there is enough absorption so that all transmission ceases. For

### Table 4. Basic reproductive ratio (\( R_0 \)) for human Immunodeficiency virus (HIV), by stage of disease*

<table>
<thead>
<tr>
<th>Stage†</th>
<th>0% migration</th>
<th>12% migration (system)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Core</td>
<td>Noncore</td>
</tr>
<tr>
<td>1</td>
<td>0.69 (25)†</td>
<td>0.12 (20)</td>
</tr>
<tr>
<td>2</td>
<td>0.10 (4)</td>
<td>0.02 (4)</td>
</tr>
<tr>
<td>3</td>
<td>0.79 (29)</td>
<td>0.20 (33)</td>
</tr>
<tr>
<td>4</td>
<td>1.16 (42)</td>
<td>0.26 (43)</td>
</tr>
</tbody>
</table>

* Based on a mathematical model. Values are shown for the core and noncore groups when there is no migration from the core group, and for the core/noncore system when there is 12% migration from the core per year. Partner mixing is assumed to be zero.
† Stages 1–4: primary infection, asymptomatic infection, symptomatic infection, and acquired immunodeficiency syndrome.
‡ Numbers in parentheses, percent contribution from each stage to the total \( R_0 \).

**FIGURE 1.** Numbers of subjects infected with gonorrhea at equilibrium, according to level of partner mixing, with zero (—) and 12 percent (- - - - - -) migration. The x-axis ranges from no partner mixing to proportional mixing. The right-hand panel shows the numbers of infected persons in the core and noncore groups (\( c_0 \) = core with 0 percent migration, \( n_0 \) = noncore with 0 percent migration, \( c_1 \) = core with 12 percent migration, and \( n_1 \) = noncore with 12 percent migration). The left-hand panel shows the totals. (Note the change in scale (y-axis) between the panels.)

gonorrhea, this happens at a level close to random mixing. For chlamydia, this point is never reached, with or without migration. However, for HIV stages 1–3, there is a huge difference in the place where this point is reached, depending on whether or not there is migration out of the core. With 12 percent migration, HIV transmission is only sustained when there is strong like-for-like partner preferences.

**DISCUSSION**

Many persons with a high partner frequency decrease their frequency over the course of life. This can be expressed as migration from the core group to the noncore group. We estimated this migration rate to be 12 percent per year. The migration will move infected subjects from the core to the noncore, reducing the prevalence in the core and increasing it in the noncore. The magnitude of these reductions/increases depends on the transmission rate and the duration of infectiousness. The three types of infections analyzed in this paper exemplify three different patterns of the effect of migration that may be summarized with the following core/noncore prevalence symbols: gonorrhea = (—/—), chlamydia = (—/↑), and HIV = (↓/↑). The migration will affect the basic reproductive ratio of diseases with a long infectious period more than that of those with a short infectious period. For HIV, this means that the later stages contribute less to the basic reproductive ratio in the presence of migration.
The results are not based on a predictive model, and are therefore qualitative in nature.

The estimate of the migration rate was based on a comparison of recent and earlier partner frequencies for each subject. The earlier partner frequency represents an average over several years, from age 16 to age 3 years prior to the survey. Older subjects have a longer period for averaging. Short periods with a high partner frequency may therefore not appear in the average measure. The m, taken from table 2 may therefore be an underestimate. Furthermore, the time under risk of migration is taken to be the total period from age 16 to age 3 years prior to the survey, which is likely to be an overestimate. Both factors lead to an underestimate of the actual migration rate. It is assumed that the core group has a constant size over time. This is corroborated by examining the size of the core in two surveys separately: 2.5 percent versus 2.4 percent. The migration rate estimate may be influenced by recall bias in the questions from which it is defined.

The present model differs from an earlier version in that HIV-infected subjects pass through four stages of infection with different transmission rates. Inclusion of this type of heterogeneity leads to a somewhat lower number of infected persons (12).

The model uses transmission rates measured per sexual act, as introduced by Dietz (13), rather than per partner. The partnerships in the noncore have, on average, five times as many acts as those in the core when there is no partner mixing (55/0.8 = 69 vs. 110/8 = 14). This leads to higher transmission rates per partner in the noncore than in the core. For infections for which the transmission rate is high, the difference is insubstantial. For infections for which the transmission rate is low, such as HIV, the difference is important. Our model therefore shows less of an effect of partner mixing than do models using a per-partner transmission estimate (2, 3). If there are aspects of behavior increasing transmission that are more prevalent in the core, our model may underestimate the effects both of partner mixing and of migration from the core. We do, however, assume a doubled HIV transmission rate in the core because of a higher prevalence of STDs acting as cofactors for HIV transmission in the core.

In this paper, results are shown for situations in which subjects with AIDS do and do not infect others. In the European partner study, 51 percent (19/37) of the couples in which the index partner had AIDS ceased having sex. Of those that did have sex with an index partner with AIDS, 71 percent used condoms consistently (14). Thus, at least for steady relationships, only a small portion of the persons with AIDS are involved in transmission.

In summary, a change in behavior among core group members leading to a migration to the noncore may have an important effect on STD levels. Depending on the rate of migration and the transmission rate and infectious period of the infection, the result may be an increase or a decrease in the total number of persons infected. Therefore, detailed knowledge of these parameters is necessary to make accurate predictions.

ACKNOWLEDGMENTS

The authors thank Wilhelm Falck for valuable help with the Appendix.
REFERENCES


APPENDIX

This appendix presents a mathematical model of sexually transmitted diseases with two activity groups, core and noncore, and $h$ stages of infectiousness. The model is an extension of a model described previously (4).

Differential Equations

The combination of group membership and stage is the state of an infected individual. The states are ordered by group (core = 1, noncore = 2) and stage ($1, \ldots, h$). Let $G = \{g_{rs}\}$ be the $2h \times 2h$ transition matrix, where $g_{rs}$ is the rate of leaving state $r$ and $g_{sr}$ is the rate of going from state $s$ to state $r$. The components of $G$ are the disease progression and the migration rates. Let $A$ be an $h \times h$ matrix describing the disease progression,

$$A = \begin{bmatrix} a_{11} & \cdots & a_{1h} \\ \vdots & \ddots & \vdots \\ a_{h1} & \cdots & a_{hh} \end{bmatrix},$$

where $a_{kk} = -\lambda_k$, $k = 1, \ldots, h$,

$$a_{k+1,k} = \lambda_k, \quad k = 1, \ldots, h-1,$$

$$a_{hh} = 0 \text{ otherwise},$$

where $\lambda_k = 1/d_k$ is the rate of leaving stage $k$ and $d_k$ is the expected duration of stage $k$. Let $K$ be an $h \times h$ diagonal matrix with the migration rate $\kappa$ on the diagonal, and let $0$ denote an $h \times h$ zero matrix. Then $G$ can be written

$$G = \begin{bmatrix} A - K & 0 \\ K & A \end{bmatrix}.$$ 

Let the rate of infection be described by the matrix $F$,

$$F = \begin{bmatrix} F_{11} & F_{12} \\ F_{21} & F_{22} \end{bmatrix},$$

where the $h \times h$ submatrices are given by

$$F_{ij} = \{f_{ij}\}, \quad f_{ij} = \begin{cases} f_{ij} = \frac{1}{n_i} (n_i - p_i) \omega_i \tau_i (1 - (1 - \beta_i \kappa)^{n_i}), & i,j = 1,2, v = 1, \ldots, h; \\ f_{ij} = 0, & i,j = 1,2, v = 1, \ldots, h, u = 2, \ldots, h. \end{cases}$$
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A. \[ p_i = \sum_{k=1}^{h} p_{ik} \], where \( p_{ik} \) is the number of infected individuals in activity group \( i \) and stage \( k \). \( \omega_i \) and \( \psi_i \) are the numbers of new partners and unprotected intercourse episodes per year in group \( i \). \( \pi_{ij} \) and \( \rho_{ij} \) are the proportions of partners and intercourse episodes that a subject from group \( i \) will have from group \( j \). \( \beta_v \) is the transmission rate per contact with an infected individual in stage \( v \), and \( c_j \) is the constant used to model the effect of cofactors on human immunodeficiency virus transmission.

The partner distribution is a preferred mixing scheme (3):

\[ \pi_{ii} = 1 - \gamma + \gamma \frac{\omega_{i1} n_i}{\omega_{i1} n_i + \omega_{i2} n_2}, \pi_{ij} = \gamma \frac{\omega_{i1} n_j}{\omega_{i1} n_i + \omega_{i2} n_2} \quad i \neq j. \]  (6)

where \( \gamma \) measures the degree of partner mixing. \( \gamma = 0 \) means no mixing; \( \gamma = 1 \) means proportional mixing.

Unless partner and intercourse frequencies are proportional in the groups, the intercourse distribution must be different from the partner distribution. The following intercourse distribution matrix is used:

\[ \{p_{ij}\} = \begin{bmatrix} 1 - \eta(\omega_{i12}/\Psi_1) & \eta(\omega_{i12}/\Psi_1) \\ \eta(\omega_{i21}/\Psi_2) & 1 - \eta(\omega_{i21}/\Psi_2) \end{bmatrix}. \]  (7)

This leads to \( \eta \) contacts in a “mixed” partnership. Because of consistency constraints, the partner distribution matrix is fully determined by \( \gamma \), and the intercourse distribution matrix is fully determined by \( \eta \).

More details on the mixing schemes can be found in Stigum et al. (4). Let \( P \) be the vector of the number of infected subjects ordered by group and stage. The number of infected persons at time \( t \) is described by the system of differential equations:

\[ \dot{P} = [F + G] \times P. \]  (8)

\( P \) and \( F \) are time-dependent; the dot over the \( P \) means differentiation with respect to time. Written out with four stages, the system looks like this:

\[
\begin{bmatrix}
\rho_{11} & f_{111} - \lambda_1 - \kappa & f_{112} & f_{113} & f_{114} \\
\rho_{12} & \lambda_1 & -\lambda_2 - \kappa & 0 & 0 \\
\rho_{13} & 0 & \lambda_2 & -\lambda_3 - \kappa & 0 \\
\rho_{14} & 0 & 0 & \lambda_3 & -\lambda_4 - \kappa \\
\rho_{21} & f_{211} + \kappa & f_{212} & f_{213} & f_{214} \\
\rho_{22} & 0 & \kappa & 0 & 0 \\
\rho_{23} & 0 & 0 & \kappa & 0 \\
\rho_{24} & 0 & 0 & 0 & \kappa \\
\end{bmatrix}
\times
\begin{bmatrix}
p_{11} \\
p_{12} \\
p_{13} \\
p_{14} \\
p_{21} \\
p_{22} \\
p_{23} \\
p_{24} \\
\end{bmatrix}
\]

Basic Reproductive Ratio

The calculation of the basic reproductive ratio \( R_0 \) follows the method given in Dietz et al. (12) and Diekmann et al. (15). Infections can be "borne" in one of two states: core, stage 1, or noncore, stage 1. To calculate \( R_0 \), we follow a newly infected subject from the core or the noncore throughout the infective period and count how many secondary cases this subject will produce on average in the core and the noncore. The resulting 2 \( \times \) 2 matrix is called the next generation operator, and \( R_0 \) equals the dominant eigenvalue of this matrix. To calculate the matrix, we need to know the rate of infection for each state and the average length of time spent in each state given the state at “birth.”

Let \( S \) be the 2 \( \times \) 2h matrix consisting of row 1 and row \( h + 1 \) of \( F \) with \( p_i \) set to zero. Then \( S \) gives the rate of infection for each state in a totally susceptible population. Let \( T \) be the 2h \( \times \) 2 matrix consisting of column 1 and column \( h + 1 \) of the inverse of \(-G\). Then \( T \) gives the expected length of time spent in each state given...
that the state at "birth" was core, stage 1, or noncore, stage 1 (16). The 2 × 2 matrix \( M = S \times T \) is the next generation operator. Written out, \( M \) looks like this:

\[
M = \begin{bmatrix}
\sum_{k=1}^{h} (f'_{1k}d_k\Omega_k + f'_{12k}(1 - \Omega_k) \sum_{k=1}^{h} f'_{12k}d_k \\
\sum_{k=1}^{h} (f'_{21k}d_k\Omega_k + f'_{22k}(1 - \Omega_k) \sum_{k=1}^{h} f'_{22k}d_k
\end{bmatrix},
\]

(10)

where

\[
\Omega_k = \left( \prod_{j=1}^{k} (1 + \kappa d_j) \right)^{-1}
\]

and \( f'_{ijk} \) denotes \( f_{ijk} \) with the \( p_i \) terms set to zero.

To examine analytically the effect of migration alone, we assume below that there is no partner mixing between the groups. The \( f_{12k} \) and \( f_{21k} \) terms are then zero. The dominant eigenvalue of \( M \) is then given by:

\[
R_0 = \sum_{k=1}^{h} f'_{11k}d_k\Omega_k,
\]

(11)

and we see directly the contribution from each stage to the total \( R_0 \) (see Jacquez et al. (9)). If, in addition, the migration rate is zero, the two groups are separate systems and the basic reproductive ratio of the noncore is given by the second eigenvalue:

\[
R_{0j} = \sum_{k=1}^{h} f'_{22k}d_k.
\]

(12)

**Equilibrium Prevalence**

The equilibrium prevalence in the core, \( p_{1*} \), is given by

\[
p_{1*} = n_1 \left( 1 - \frac{1}{R_0} \right).
\]

(13)

We arrive at an approximate formula for the equilibrium prevalence in the noncore:

\[
p_{2*} = \kappa \Phi_1 + \kappa D \frac{\Phi_2}{1 - R_{0j}},
\]

where

\[
D = \sum d_k, \quad \Phi_1 = \sum_{k=1}^{h} d_k \sum_{j=1}^{k} p_{1j}^*, \quad \text{and} \quad \Phi_2 = \sum_{k=1}^{h} f_{22k}d_k \sum_{j=1}^{k} p_{1j}^*.
\]

(14)

The approximation holds when \( R_{0j} < 1 \) and the saturation term \( (n_2 - p_2)/n_2 \) is close to 1.