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Estimation of the forces of infection in a complex epidemiological model for meningitis using genetic algorithms

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1. Epidemiology modelling of meningitis

The epidemiology of meningococcal meningitis, whose aetiological agent is the bacterium Neisseria meningitidis, is highly complex. This complexity derives from the high genetic and antigenic variability of Neisseria meningitidis, the unclear mechanisms causing disease given infection (especially those regarding the interactions between the pathogen and the host immune defenses), and the ecological competition between different serogroups of meningococci and with a related non-pathogenic bacterium, called Neisseria lactamica.

Up to date, the only mathematical model used to evaluate the effects of the strategies of control of meningococcal meningitis is that of Trotter et al. [1], which has been designed to assess the impact of the vaccination campaign against the C serogroup, applied by the UK government since 1999. This is an age-structured SIS model which includes the ecological competition for the colonization of susceptible hosts between the C serogroup and other serogroups, including Neisseria lactamica. The model includes the vaccination at birth or during a catch-up program. As suggested by the current evidence, the vaccine is assumed to be ineffective against infection by the meningococcus and the consequent acquisition of carriage, but to be protective against the development of meningococcal disease, which is only an accidental and rare outcome of infection.
In order to avoid the problem, very common in models with competition between pathogens, of the instability of the equilibrium of coexistence, the only "truly" dynamic force of infection in the model is that of the serogroup C. In fact, while the force of infection (FOI) for the serogroup C in this model is calculated from the number of carriers in each age group, weighted by the elements of the WAIFW matrix, the FOI of the other serogroups is time-invariant.
Such assumption is justified with the observation that the carriage of C meningococci represents only a small percentage of carriage of all meningococci, and so its dynamics should not affect significantly the other FOIs. Anyway, this is the only manner to ensure dynamic coexistence for arbitrary parameter constellations. The 'equilibrium FOIs', including that for the C serogroup, had been calculated by Trotter et al. in a previous article [2] from historical carriage data by Cartwright et al. (UK, 1986) [3] and Gold et al. (USA, 1972) [4].

2. The model

In this article, Trotter et al. use a model that includes the competition of four bacterial strain, representing meningococcal serogroups B and C, other meningococcal serogroups (O), and the non-pathogenic Neisseria lactamica (L); the model used is a Schenzle-type age-structured, competitive SIS model with 75 one-year-wide classes. Trotter et al. assume that the carriage prevalence data, which show nonzero prevalences for all of the four competitors, may be considered as equilibrium data of their model; if this is true, the force of infections of the groups, at equilibrium, depend only on the age group. Thus, they impose a functional form with five parameters for the force of infection of each group, and compare the real data with the equilibrium prevalences predicted by the

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model with each parameter set, in order to obtain a maximum likelihood estimate of the model parameters.

The model used for the estimation of FOIs can be described by the following linear system of ordinary differential equations:

$$\begin{aligned} \dot{x}_a(t) &= -\lambda_a x_a(t) + \sum_{s=B,L,O,C} (\gamma_s y_{sa}(t)) \qquad with\ \lambda_a = \sum_{s=B,L,O,C} \lambda_{sa} \\ \dot{y}_{sa}(t) &= \lambda_{sa} x_a(t) - \gamma_s y_{sa}(t) \qquad for\ \ s=B,L,O,C \end{aligned} \quad (1),$$

where

$x_a(t)$ is the fraction of susceptible individuals in each age group a at time t;

$y_{sa}(t)$ is the fraction of infectious individuals in each age group a and for each strain s at time t;

λ_a is the total force of infection at equilibrium of the four strains;

λ_{sa} is the force of infection at equilibrium for strain s;

γ_s is the rate of recovery from carriage for strain s;

For the 4 strains and the 75 age groups considered, the model includes 75 x 5 equations.

According to the model of Schenzle, after t=1 year, all the susceptibles and infected are wholly transferred in the corresponding class of the next age group; those being in the last age group (a=74) die, and an equal number is inserted in the susceptible class of the first age group. That is, the mortality rate is 0 for all ages except for a = 74, where it is infinite.

Anyway, for the calculation of the equilibrium values, it is not necessary to introduce this mechanism of age-structure, and it will be sufficient to calculate the equilibrium values of the equations (1), where the age groups are intended simply as population groups, without aging. In fact, what the Schenzle-type dynamics introduce is only an instant change, occurring at the beginning of every new year, in the initial values of the variables in each age-group, while the equilibrium of a dynamic linear system is indipendent from initial values.

3. The functional form of the FOI

The functional form adopted by Trotter et al. to establish the values of λ_{as} is given by the formula:

$$\lambda_{as} = 12\left(b_s + \frac{c_s - b_s}{1 + e^{\frac{-(a-T_s)}{\omega_s}}}\right)\left(1 + \frac{d_s - 1}{1 + e^{\frac{-(a-T_s)}{\omega_s}}}\right) \quad (2),$$

where a is expressed in years, and b_s, c_s, d_s, T_s, ω_s are the 5 parameters to be estimated for each group. The unit of measure of b and c is the year^{-1}, that of T and ω is the year, while d is a pure number.

We can interpret this functional form as the product of two sigmoid functions $\lambda_1(a)$ and $\lambda_2(a)$:

$$\lambda_1(a) = 12\left(b_s + \frac{c_s - b_s}{1 + e^{\frac{-a-T_s}{\omega_s}}}\right),$$

$$\lambda_2(a) = \left(1 + \frac{d_s - 1}{1 + \frac{e^{-(a-T_s)}}{\omega_s}}\right).$$

A sigmoid function is a smoothed step-function, going monotonically from an asymptotic value to another with null derivative at $\pm\infty$. In our case the asymptotic values of the two functions are:

$$\lambda_1(-\infty)=12\,b_s \qquad \lambda_1(+\infty)=12\,c_s$$
$$\lambda_2(-\infty)=1 \qquad \lambda_2(+\infty)=d_s$$

The two sigmoids have a common inflection point at a = T_s, and the slope of the 'smoothed step' is determined by ω_s.

In order to obtain a peak in the FOI, given by the product of the two sigmoids, it is necessary and sufficient that the derivatives of $\lambda_1(a)$ and $\lambda_2(a)$ have an opposite sign (remember that the two functions are strictly monotonic); this is equivalent to say that:

$$c_s > b_s \quad if \quad d_s < 1 \quad , \text{or} \quad c_s < b_s \quad if \quad d_s > 1 \quad .$$

Under these conditions, there will be a peak at age $a=T_s$ and its width will be determined by ω_s. The other parameters of the functional form have no clear physical meaning: b_s gives an idea of the value of the FOI at a = 0; c_s and d_s indipendently have no meaning at all, but their product influences the value of the FOI at a = 74. The actual values of the FOI at the limits of the dominion, anyway, are heavily affected by the position and width of the peak.

On the whole, this choice of the FOI by Trotter et al. seems rather arbitrary, as it introduces a high number of parameters respect to the more common Farrington function (with three parameters); moreover, some of the parameters have no clear physical significance. Nonetheless, in the course of this work we have kept to this form, in order to replicate and comment the results of their studies.

4. Estimation of FOIs through standard methods

The other parameters of the model, that is the rates γ_s of recover from carriage, were assumed constant with age and time. Their values were suggested explicitly for the different serogroups by the literature data on duration of carriage and set to 1.333 $years^{-1}$ for $s = B, O, C$ and to 3 $years^{-1}$ for $s = L$; these values correspond to a duration of carriage of 9 months for the meningococci and 4 months for the Neisseria lactamica; it should be pointed out, anyway, that the distributions of the duration of carriage in real data are deeply different from the exponential. Moreover, there are consistent clues that the duration of C is shorter (3 months) than that used in this model, and the results of Trotter et al.'s model with vaccination also confirmed this suggestion. Thus, one objective of our study was to recalculate the fitting process, in order to determine whether using this shorter duration changes significantly the FOIs of the other groups, which in turn would affect heavily the results of the model with vaccination.

The prevalences predicted by the model were used to maximize the logarithmic likelihood associated to the set of parameters tried, according to the formula:

$$\log L = \sum_{s=B,L,O,C} \sum_{a} (Y_{as} \log y_{as}(\infty)) + \sum_{a} (X_a \log x_a(\infty)) \quad (3),$$

where X_a, Y_{as} are the empirical data on prevalence of susceptibles and infectives for the 4 groups, while $x_a(\infty)$ and $y_{as}(\infty)$ are the predictions of the model.

The method of likelihood maximization has statistical grounds: at first, we assume that the equilibrium prevalences predicted by the model, $x_a(\infty)$ and $y_{as}(\infty)$ are correct, so that they may be interpreted as the probability that each individual of age a has to end up in the class of the susceptibles or of the infected with one of the four bacterial strain. The probability to observe the empirical data (Y_{as} and X_a) given the probability of each class may be calculated through the following expression:

$$L(b_s, c_s, d_s, T_s, \omega_s) = \prod_a x_a(\infty)^{X_a} y_{aB}(\infty)^{Y_{aB}} y_{aL}(\infty)^{Y_{aL}} y_{aO}(\infty)^{Y_{aO}} y_{aC}(\infty)^{Y_{aC}} \quad (3a).$$

In fact, the composite probability of two indipendent events is given by $P(A \cap B) = P(A)P(B)$. In our case the events are represented by an individual belonging to its class of infectivity: for example, the probability that X_a individuals (for each age group) will belong to the class of the

susceptibles, is given by the product of the X_a probabilities $x_a(\infty)$ that each of the individuals considered has to end up in that class; this product is actually the quantity $x_a(\infty)^{X_a}$. Extending this reasoning to the 4 classes of infected and to all age groups, we obtain the expression (3a), which is called the *likelihood* of the model.
The likelihood gives an information on how much it is likely that the observed data would happen, given the probabilities predicted by the model. Anyway, we are sure only of the correctness of the data (assuming that the measurement errors are negligible), and not of the model predictions: for a model which describes correctly the reality, we would expect a high value of the likelihood, especially when the number of observation is high. Thus, maximizing the likelihood means to obtain the parameter set that best justifies the observed data.
For computational reasons it is generally more convenient to calculate the logarithm of the likelyhood: applying the properties of the logarithms to equation (3a) gives straightforwardly equation (3).

The maximization of this function is not trivial. Using a commercial spreadsheet editor, Trotter et al. have found the following optimal values for the parameters:

Parameter/Group	B	L	O	C
b	$8.15\ 10^{-4}$	$1.00\ 10^{-6}$	$4.16\ 10^{-4}$	$1.69\ 10^{-4}$
c	$6.23\ 10^{-2}$	0.214	$8.08\ 10^{-2}$	$1.22\ 10^{-2}$
d	$6.76\ 10^{-2}$	$2.92\ 10^{-2}$	$7.85\ 10^{-2}$	$2.69\ 10^{-2}$
T	18.667	2.417	17.917	17.25
ω	1.667	1.083	3.75	1.417

Table 1: best fitting parameters according to Trotter et al.

The graphs of the FOIs corresponding to this set of parameters are displayed in a semilogarithmic plot in figure 1 (B: blue, L: magenta, O: cyan, C: red). We can notice that the FOI of Neisseria

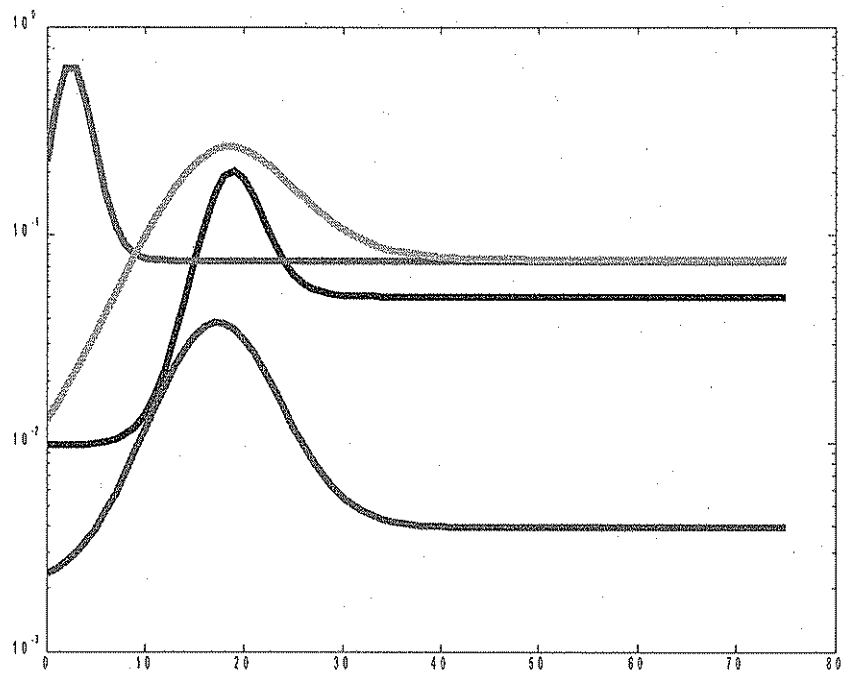

Figure 1: FOIs found by Trotter et al.

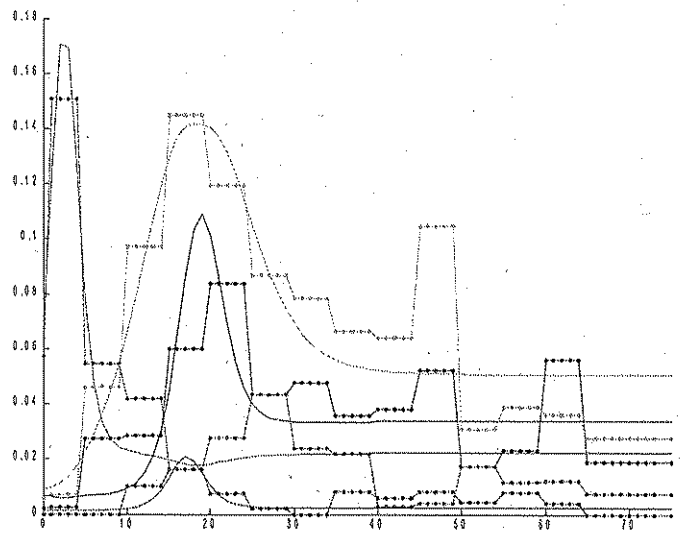

Figure 2: Trotter et al.'s predictions of the age-profiles of equilibrium prevalences

lactamica has an early peak at 2.417 years and remains constant and relatively high after 10 years; the meningococcal serogroups all reach a peak between ages 17 and 19, with a much lower activity by the C serogroup and a significantly broader peak by the 'other' strains (O).
In figure 2 we represent the predictions for the different age groups, compared with real data as provided by Trotter et al. [2] (grouped in 15 uneven age groups); the dotted lines represent real data, while the solid lines are the predictions of the model.

5. Genetic algorithms

The primary objective of our study was to replicate the estimate by Trotter et al. in order to obtain analogous results and to check their robustness respect to the hypoteses assumed. The tool that was used for the maximization of the likelihood is a Matlab program that implements a genetic algorithm.

Genetic algorithms mimick the process of genetic evolution (which occurs through reproduction, mutations and selection of best-performers) to maximize any given fitness function, however complex. Given a generic vector of parameters x, with dimension n, and a scalar *fitness function* $f(x)$, the genetic algorithm looks for the x_m in the dominion where $f(x_m)$ is highest. In our case, the fitness function will be given by the likelihood as expressed in formula (3).
Genetic algorithms are an extremely general purpose tool, and they are able to find the global maximum of the function starting from any initial point in the dominion, through a guided exploration in the whole dominion of existence of the function.

There are several versions of genetic algorithms, all based on the same principles. We give here the version that was used in our study.
The starting point of a genetic algorithm is the definition of an initial population of N *chromosomes*, each of which is an appropriately formatted input vector of the fitness function; each element of the chromosome is called a *gene*. The value of the fitness is calculated for each chromosome, and the first e best-scoring chromosomes are selected and copied in the pool of the next-generation population (*elitism*). The remaining chromosomes of the next-generation population are obtained

from the mechanism of *reproduction*. We pick *N-e* chromosomes from the whole original population, with a probability proportional to their fitness value; each chromosome may be picked more than once. The picked chromosomes, coupled by two, will give birth to two new 'sons', each of which inherits the genes of both parents. In our study, this passage is implemented by a mechanism of *cross-over*, which creates two new chromosomes: one whose first *g* genes come from 'the father' and the remaining *n-g* from the mother, and the other whose first *g* genes come from 'the mother' and the remaining *n-g* from the father. The number *g* is chosen at random at each reproduction.

The *e* chromosomes selected through elitism, and the *N-e* sons generated by an equal number of parents, constitute the next-generation population, which conserves its dimension N. Each chromosome of the new population may undergo *mutation*, with a certain fixed probability *p*. Mutation implies a variation in an element of the chromosome that should not include the exchange of genetic information with others; this passage allows for the exploration of possible solutions even in a dominion outside that of the initial population. Anyway, given the format of the chromosomes in the present case, we have implemented it as the exchange of elements at position g_M (again, randomly chosen) between two successively indexed chromosomes.

In this way, the next-generation population includes different chromosomes (which allows to explore new regions of the dominion) that on average should perform better than the previous generation, provided that the mutation rate is kept sufficiently low. This process is iterated until convergence (i.e. unchanged value of fitness for the best performer for a certain number of epochs) or until the maximum number of epochs is reached.

We can thus say that the ability of genetic algorithms to find the maximum of a function is given by the fact that, for each generation, the dominion where we look for the maximum is extended in a manner that is not random, but guided by the value of the fitness itself: at each generation the points of the dominion to be tested are spread over an area around the best scorers, and the new points that most successfully combine the characteristics of the parents are selected for a more detailed exploration of the area around them. The mutation process may move the exploration in a 'virgin' area of the dominion, causing in some cases the non-monotonic growth of the best-performer fitness; this would correspond to the possibility of episodes of regression of the population, instead of evolution. Anyway, mutation is useful to provide a wider exploration of the dominion of existence of the function, making the algorithms less vulnerable to local maxima.

6. Estimation of FOIs through genetic algorithms

In our case, the chromosomes are vectors of $n = 20$ elements (genes), corresponding to the parameters of Table 1 taken by column: first the 5 parameters for group B, then those for group L, O and finally C.

To define the initial population, we build a pool of chromosomes containing genes that cover a wide neighbourhood of the best-fitting set found by Trotter et al.

To do this, we defined a matrix *S* with $N = 51$ columns all equal to the set of Table 1. We have then defined two row "multiplier" vectors m_l and m_a, made by 51 logarithmically spaced coefficients in the range from $Kl_{min} = 10^{-2}$ to $Kl_{MAX} = 10^2$ for m_l and from $Ka_{min} = 0.2$ to $Ka_{MAX} = 5$ for m_a. These vectors are used to build a 51x20 "multiplier" matrix *M*, so that the rows corresponding to b_s, c_s, and d_s (rows number 1+5k, 2+5k, 3+5k with k=0,1,2,3) were filled with vector m_l, and those corresponding to T and ω (rows 4+5k, 5+5k, with k=0,1,2,3) were filled with vector m_a. Finally, the starting population was obtained from the columns of matrix *C*, given by the element-wise multiplication of matrices S and M. In this way the starting population allows to explore a wide neighbourhood of the chromosome obtained from Table 1, as it contains genes which cover a range of Kl_{min} to Kl_{MAX} of b_s, c_s, and d_s and of Ka_{min} to Ka_{MAX} of T_s and ω_s. The interval of values for T_s and ω_s is narrower because these parameters represent respectively the age of peak of the FOI and

the width of this peak, so their values will undergo only relatively small excursions, being the age axis confined to a 0 to 75 year range.

The genetic algorithm was implemented through a Matlab program. The calculation of the fitness required to calculate the equilibrium prevalences $\bar{x}_a$ and $\bar{y}_{as}$, which in this case can be computed in closed form.

For a generic age group a, the equations in $\dot{y}_{as}$ at equilibrium give:

$$0 = \lambda_{as}\bar{x}_s - \gamma_s \bar{y}_{as} \rightarrow$$
$$\rightarrow \bar{y}_{as} = \frac{\lambda_{as}}{\gamma_s}\bar{x}_a \quad , (4)$$

where for the conservation of the total population, $\bar{x}_a = 1 - \sum_s \bar{y}_{as}$. By substituting in equation (4), defining $\sigma_{as} = \frac{\lambda_{as}}{\gamma_s}$ and rearranging we obtain:

$$\bar{y}_{as}(1+\sigma_{as}) + \sigma_{as}\sum_{z\neq s}\bar{y}_{az} = \sigma_{as} \quad .$$

The equations, explicited for s = B, L, O and C, represent a 4x4 linear system of the form

$$A_a \bar{y}_a = \sigma_a \quad ,$$

where $\sigma_a = \begin{bmatrix} \sigma_{aB} \\ \sigma_{aL} \\ \sigma_{aO} \\ \sigma_{aC} \end{bmatrix}$, $\bar{y}_a = \begin{bmatrix} \bar{y}_{aB} \\ \bar{y}_{aL} \\ \bar{y}_{aO} \\ \bar{y}_{aC} \end{bmatrix}$ and $A_a = \sigma_a \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \end{bmatrix}^T + I$,

and I is the identic matrix. The final prevalence predicted by the models can then be calculated by simple algebra which requires only the inversion of the 75 matrices A_a associated with each age group, and their multiplication with vector σ_a. This is easily integrated into the genetic algorithm and justifies their suitability for this kind of maximization: in fact, genetic algorithms require, to work quickly, that the computational burden of the calculation of the fitness is not too

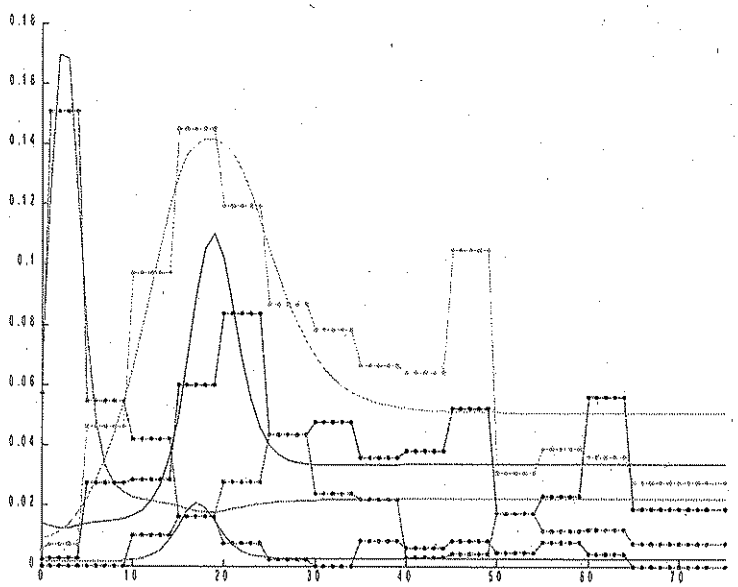

Figure 3: predictions of the model with the best-fitting parameter set found by genetic algorithms

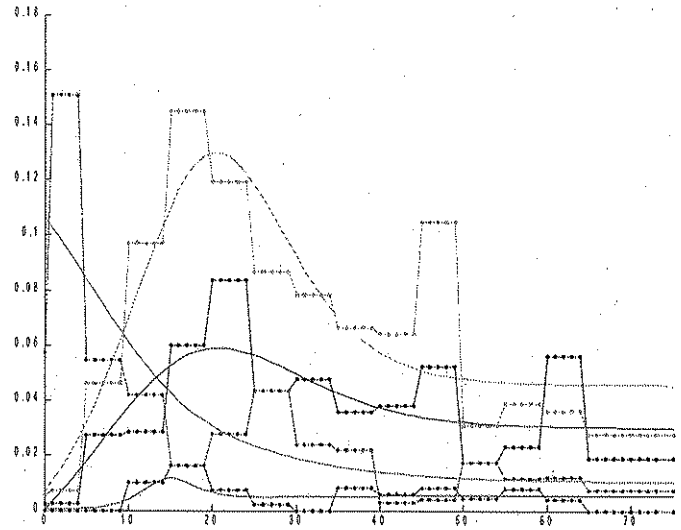

Figure 4: predictions of the model with the best-fitting parameter set found by Matlab's built-in function fminsearch

heavy, as this calculation must be repeated for each of the N chromosome and for hundreds of iterations.

In figure 3 we show the results obtained with 100 iterations of the genetic algorithm, which allow a good convergence in approximately the same time as the Matlab built-in function fminsearch. The dotted lines represent the real data grouped in 15 classes as provided by the article by Trotter et al.; the raw data divided in 75 age classes were not available. The solid lines represent the age profiles of the final infected for each serogroup (B: blue, L: magenta, O: cyan, C: red) as predicted by the model with the best-fitting parameter set.

This graph may be compared with the best results by the fminsearch, shown in figure 4, where the starting point in the parameter dominion was taken as the set of Table 1.

It is apparent that the fminsearch algorithm misses the peak of carriage of Neisseria lactamica, and underestimates the height of the peaks of meningococcal carriage respect to the genetic algorithm.

Anyway, the value of likelihood is nearly the same for the two algorithms (log L = -39.65 for fminsearch and log L= -39.75 for the genetic algorithm with the specified settings).
The result of the genetic algorithm after 100 iterations is very similar to that obtained by Trotter et al., as is shown by the figures 5-8. They represent the FOIs predicted by the genetic algorithm (solid blue lines) and those predicted by Trotter et al (black dots). The cyan lines represent the FOI obtained with a duration of serogroup C carriage of 3 months instead of the base case of 9 months. In the scenario of a shorter duration of C carriage, we can see that a consistent change happens only for the C serogroup, resulting in a wider peak and not in an upward translation of the FOI. Although the parameter estimations in this case are different for the group C than in the base case, the predictions of figure 6 remain practically unchanged. The FOIs for serogroup B, L and O are substantially superimposed to those of the base case.

7. Discussion

We have replicated the calculation of the FOIs through the fitting of the parameters to the

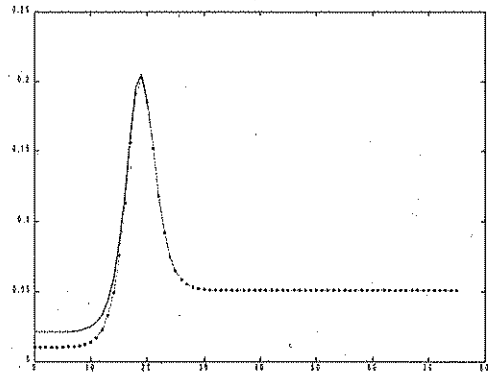

Figure 5: FOI for group B

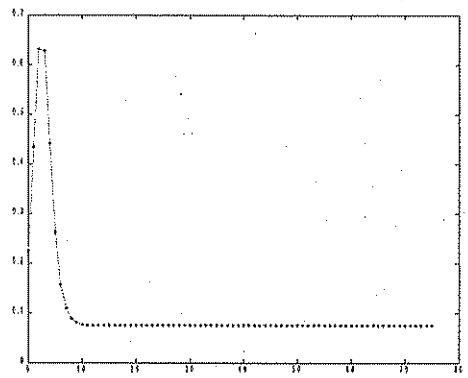

Figure 6: FOI for group L

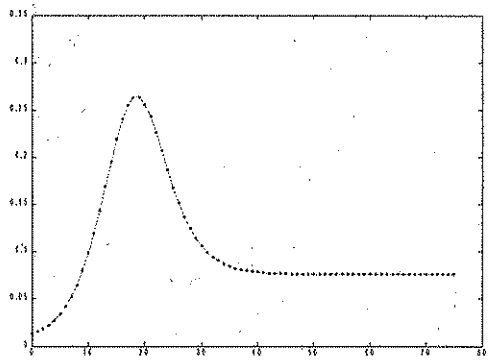

Figure 7: FOI for group O

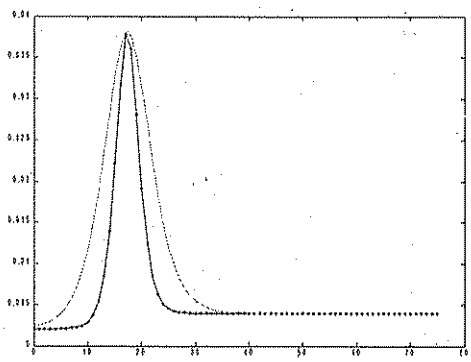

Figure 8: FOI for group C

equilibrium predictions of a SIS model with 4 competitors and a Schenzle-like age structure with 75 cohorts. Differently from Trotter et al., we have used a genetic algorithm to maximize the likelihood of equation (2), which was the quality indicator adopted for the measurement of the fitness of the parameter set. Moreover, we exploited the fact that Schenzle's age structure may be neglected, as the equilibrium values are indipendent by the yearly shifting of the age groups: this has allowed to calculate the equilibrium prevalences of the model through simple matrix inversions for each age-group.

Genetic algorithms are very general purpose maximization tools, but the speed of their convergence is particularly sensible to the many settings to choose: the starting population, the number of chromosomes in the population, the elitism parameter e, the reproduction mechanism, the mutation mechanism and probability.

With the settings proposed, the genetic algorithm has proved to be an efficient tool, as it converged to the maximum values in less than 100 iterations, taking a total running time which was on average slightly smaller (10%) respect to the Matlab built-in function fminsearch. Its results in terms of total likelihood were also at the same level as fminsearch, but they agreed much better with the results by Trotter et al., although the initial conditions were taken for both in the same region, around Trotter et al.'s estimation.

With the algorithm described, we were also able to re-calculate the FOIs of the 4 groups assuming as an average duration of C carriage of 3 months, instead of 9 months, as suggested by recent epidemiological literature and by the results of the model with vaccination by Trotter et al themselves. We have found out that the FOI for the C group presented a wider amplitude of its peak (2.85 years compared to 1.42 years of the base case), and not an upward translation of the base-case FOI, while the FOIs for the other three serogroups remained unchanged. This means that a shorter

duration of C serogroups will introduce a greater incidence especially in the age groups around the peak (17.25 years).
These results support the use of FOIs calculated with a C duration of 9 months in the model with vaccination of Trotter et al., as the only FOI which would vary with a shorter duration of C is the one of the C serogroup; anyway, this FOI varies dynamically with the number of carriers in the model with vaccination.

Finally, we have to point out that the assumptions that the data are at equilibrium, which allows to consider carrier-indipendent FOIs, has not been justified, and **is not confirmed** by dinamical simulations with carrier-dependent FOIs of the model structure described. In fact, the dynamical competition between serogroups would bring to the exclusion of one or two groups with many different duration of carriages, resulting in a weak coexistence of the 4 serogroups only for very narrow intervals of the carriage durations.
The model structure responsible for the coexistence of serogroups is yet to be found; although Trotter et al.'s predictions show good agreement with the follow-up data of the UK vaccination strategy, no reliable conclusion on control strategies may be grounded in the absence of a realistic model structure.

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