

Modelling vector-host disease transmission and food web dynamics through the mixing/pair formation approach

*Jorge X. Velasco-Hernandez
and Carlos Castillo-Chavez*

Abstract. In this article we apply recently developed mixing/pair formation structures to the modelling of frequency predator-prey interactions. Applications to vector-host interactions and food web dynamics are provided.

1. Introduction

During the last ten years, mainly due to the spread of HIV/AIDS throughout the world, there has been a surge of mathematical studies on the population interactions involved in the transmission of infectious agents. In particular, the study of sexually transmitted diseases has motivated models of the mechanisms of pair formation and mixing among individuals belonging to heterogeneous populations (populations structured in groups characterized by different levels of sexual activity, drug use, etc.). The mechanism of pair formation has been formalized by Castillo-Chavez and collaborators [see Castillo-Chavez and Busenberg (1991); Busenberg and Castillo-Chavez (1991), Blythe and Castillo-Chavez (1989), for example] among others, through an axiomatic approach. They postulate a series of axioms for the mixing probabilities and a conservation property on the number of contacts per unit time between interacting individuals belonging to different subgroups. This postulate is the key component used on generalization of the approach to other population processes. Two of these applications are reviewed in this work. Vector-host interactions constitute, perhaps, the most immediate application of the framework since they are analogous to male-female encounters in a two-sex population. The first documented attempt to establish a conservation of contacts property was provided by Ronald Ross in his studies of Malaria (Ross, 1911). The second example is of predator-prey interactions structured through frequency dependent functional responses. Lotka Volterra models of food webs assume that predation rates follow the mass action law, i.e. the predation rate is directly proportional to the density of prey. Shortcomings of this assumption are

found in the literature (see Ariditi and Ginzburg, 1989). The approach discussed in this manuscript provides alternative descriptions.

The paper is organized as follows: Section 2 provides a brief description and discussion of the classical Ross-Macdonald model of Malaria transmission; Section 3 provides a modeling framework for the building models for vector-transmitted diseases using the pair formation/mixing approach of Busenberg and Castillo-Chavez (1991); Section 4 provides an application to food web modelling; in Section 5, we give our conclusions.

2. The Ross-Macdonald model

Epidemiology was one of the first areas of research in biology where mathematical models were successfully applied. The basic formulas for the estimation of biting rates and associated parasite transmission rates were built after Ross' studies in the population dynamics of Malaria (Ross, 1911). The factors affecting transmission in vector transmitted diseases can be summarized as follows (Molineaux, 1988):

- 1) The density of vectors with respect to humans,
- 2) The effectiveness of the vector in acquiring and maturing the infection,
- 3) The frequency of blood meals,
- 4) The fraction of blood meals taken from human hosts,
- 5) The incubation period of the parasite in the vector,
- 6) The longevity of the vector.

Most of these factors have been included in a single parameter that is a measure of how effective is a given vector population in transmitting the infection agent to its host. The *vectorial capacity* is defined as the capacity of the vector to transmit the disease in terms of the potential number of secondary inoculations originating per day from an infective person (Molineaux, 1988). The formulation of vectorial capacity given by Macdonald (1957) is

$$C = \frac{ma^2p^n}{-\ln p}$$

where

m is the ratio of vector to host numbers,

a is the biting rate (number of blood meals per host per day).

p is the proportion of vectors surviving per day.

n is the length (in days) of the parasite incubation period in the vector.

By multiplying this expression by r^{-1} , the expected duration of infectiousness in the host, we obtain the basic reproductive number

$$R_0 = \frac{C}{\mu r}$$

where we have defined $p = e^{-\mu}$, μ being the daily vector death rate with

$$C = \frac{ma^2e^{-\mu}}{\mu}.$$

This basic reproduction number and its associated model, have provided useful insights in the study of the population dynamics of infectious diseases. However, it is based on assumptions that need to be modified for its useful implementation to disease transmission in heterogeneous populations where demographic activity is not negligible. The limitations are better understood after one analyzes the main assumptions behind the Ross-Macdonald formulation. They are:

- 1) The vector is fully effective in acquiring and maturing the infection.
- 2) The vectors die at a constant rate.
- 3) Longevity is not affected by infection.
- 4) The probability of feeding is not affected by the number of previous meals.
- 5) The probability of feeding is not affected by the number of host types.
- 6) Parasite presence does not affect preference.

To take into account heterogeneity, we may need to consider:

- a) Behavioral aspects of the vector. In particular we probably need to take into account the time budgeting of vectors (eg., foraging and search time) thus introducing multiple time scales into the models.
- b) Diversity of host types (different degree of susceptibility)
- c) Frequency dependent contact rates. Not all host types are equally abundant and this implies that the frequency at which a given host type is bitten may depend on its relative frequency.
- d) Vector preference, understood as the differential budgeting of biting rates among host types.

Examples of diseases where these factors are important include Dengue, Malaria, Chagas' disease and Leishmaniasis.

3. Modelling vectorial transmission

We model the situation in which we have several types of interacting vector and host subpopulations. Let N_i denote the total human population of town i and $T_k = W_k + V_k$ the population of vectors of species k where W_k and V_k represent the susceptible and infective subpopulations respectively. In this model we assume that vector species are not regulated by disease density. Also, we assume that vectors' carrying capacities have values distributed according to a given probability density. Thus we denote by q_{ki} the probability that species k enters into contact with group i of hosts. We assume that the host group has a constant recruitment rate Λ_i and we arbitrarily set the disease induced mortality rate equal to zero. With

this assumptions we have the following set of equations for host-vector interactions:

$$\begin{aligned}
 S_i &= \Lambda_i - B_i^N(t) + \gamma I_i - \mu S_i, \\
 I_i &= -(\mu + \gamma) I_i + B_i^N(t), \\
 W_k &= g(T_k)[\beta T_k - \delta W_k] - B_k^T(t), \\
 V_k &= -g(T_k)\delta V_k + B_k^T(t).
 \end{aligned} \tag{1}$$

for $i = 1, \dots, n$ and $k = 1, \dots, m$.

Where

$$B_i^N(t) = a_i^T S_i \sum_{k=1}^m p_{ik}(t) \rho_k \frac{V_k}{W_k + V_k},$$

denotes the i -th host incidence rate, and

$$B_k^T(t) = a_k^N W_k \sum_{i=1}^n q_{ki} \lambda_i \frac{I_i}{S_i + I_i},$$

represents the k -th vectorial incidence rate. In addition, ρ_k and λ_i are coefficients that measure, respectively, the infectivity of vectors and hosts; a_j^x represents the average number of contacts with population x by members of group j ; $p_{ik}(t)$ is the probability of contact of hosts of group i with vectors of species k at time t ; $q_{ki}(t)$ is the probability of contact of vectors of species k with hosts of group i . These probabilities constitute a mixing matrix.

Definition 1 (Castillo-Chavez and Busenberg, 1991) The matrix (p_{ik}, q_{ki}) is called a *mixing/pair formation matrix* if and only if it satisfies the following properties:

1. $0 \leq p_{ik} \leq 1$, and $0 \leq q_{ki} \leq 1$,
2. $\sum_{k=1}^m p_{ik} = 1 = \sum_{i=1}^n q_{ki}$,
3. $a_i^T N_i p_{ik} = a_k^N T_k q_{ki}$, for $i = 1, \dots, n$ and $j = 1, \dots, m$.
4. If for some i , $1 \leq i \leq n$ and/or some j , $1 \leq j \leq m$ we have that $a_i^T a_k^N T_k N_i = 0$, then we define $p_{ik} \equiv q_{ki} \equiv 0$.

Condition (3) is interpreted as a conservation of contact rates law or group reversibility property while (4) asserts that the mixing of inexistent subpopulations, either of hosts or vectors, cannot be arbitrarily defined.

The axioms stated in Definition 1 were motivated by the study of the sexual/social mixing structures that determine the transmission of sexually-transmitted diseases, especially AIDS. These axioms incorporate natural constraints that occur during the transmission process. In particular, Busenberg and Castillo-Chavez (1991) have shown that all mixing probabilities that satisfy the axioms in Definition 1 can be obtained as multiplicative perturbations of a special family of solutions called *separable* solutions (see Definition 2 below). Separable solutions describe proportionate or random mixing. The framework formalized by Busenberg and Castillo-Chavez (1991) is general enough as to include all the major mixing processes used in modeling contact patterns for the transmission of infectious and sexually-transmitted diseases and can be adapted to deal with contact patterns for vector transmitted diseases. In the next sub-section we derive expressions for

the mixing probabilities for contacts such as those associated with vector-host interactions.

3.1 Derivation of the contact probabilities

Let C_{ij} represent the number of contacts per day of a vector of species i with a host of group j for $i = 1, \dots, m$ and $j = 1, \dots, n$. Then, necessarily

$$T_i C_{ij} = N_j C_{ji}.$$

Let τ_i be the total time spent foraging by an average vector of species i , and denote by σ_{ij} the handling time spent by a vector of species i on hosts in group j . Then

$$\tilde{\sigma}_i = \sum_{k=1}^n \sigma_{ik} C_{ik}, \quad (2)$$

is the mean handling time of vectors of group i . Now, the searching time of vectors of type i is $\tau_i - \tilde{\sigma}_i$; this is the time that vectors of species i have to find host suitable for blood meals. Hence, the number of contacts that an average vector of type i has with hosts in group j is

$$C_{ij} = (\tau_i - \tilde{\sigma}_i) \beta_{ij} N_j. \quad (3)$$

Here β_{ij} is the rate of successful contacts (contacts that result in a blood meal) of vector species i with hosts of group j which we assume a function of the total number of vectors feeding in average on a host of group j . Let T_{*j} be the average number of vectors (all species included) feeding on hosts of group j . Assume

$$\beta_{ij} = \frac{b_{ij}}{T_{*j}},$$

which reflects the fact that vectors are less efficient in contacting a host as the density of vectors per host increases. We impose the condition $b_{ij} = b_{ji}$ for i, j within the common range of indices.

Substituting now (2) in (3) we obtain

$$\tilde{\sigma}_i = (\tau_i - \tilde{\sigma}_i) \sum_{k=1}^n \sigma_{ik} b_{ik} m_k,$$

where

$$m_k = \frac{N_k}{T_{*k}}$$

is the ratio of hosts to vectors in the k th host group which we call the *Ross ratio*. Solving for $\tilde{\sigma}_i$ we obtain

$$\tilde{\sigma}_i = \frac{\tau_i \sum_{k=1}^n \sigma_{ik} b_{ik} m_k}{1 + \sum_{k=1}^n \sigma_{ik} b_{ik} m_k}, \quad (4)$$

and then substituting into (3) and after some algebra we have

$$C_{ij} = \frac{\tau_i b_{ij} m_j}{1 + \sum_{k=1}^n \sigma_{ik} b_{ik} m_k}.$$

To compute p_{ij} we use the formula $\frac{C_{ij}}{C_i}$ where $C_i = \sum_{j=1}^n C_{ij}$. Thus, the probability of effective contacts between a vector of species i and a host of group j is

$$p_{ij} = \frac{b_{ij} m_j}{\sum_{j=1}^n b_{ij} m_j}. \quad (5)$$

To derive the probability q_{ji} of effective contacts of hosts of group j with vectors of species i we use the relation $T_i C_{ij} = N_j C_{ji}$ to solve for C_{ji} . After some algebra and the use of the formula $q_{ij} = \frac{C_{ji}}{C_j}$ we obtain

$$q_{ij} = \frac{\tau_i b_{ij} T_i}{1 + \sum_{k=1}^n \sigma_{ik} b_{ik} m_k} / \sum_{i=1}^m \frac{\tau_i b_{ij} P_i}{1 + \sum_{k=1}^n \sigma_{ik} b_{ik} m_k}. \quad (6)$$

By construction, (5) and (6) satisfy the set of axioms (1) to (3) above (axiom (4) is satisfied by definition) hence, they are particular forms of the general solution of Castillo-Chavez and Busenberg (1991). Formula (6) may be interpreted in the following way: b_{ij} is the maximum biting rate when no density dependent effects are taken into account so, $\tau_i b_{ij} T_i$ is the number of bites made by vectors of type i on hosts in group j during the total foraging time characteristic of the vector species. The numerator of (6) gives the proportion of bites on all hosts corresponding to vectors of species i ; the denominator represents clearly the total number of bites made on all hosts by all types of vectors.

Notice that p_{ij} depends only on the Ross' ratio and that q_{ij} depends on the Ross' ratio as well as on the handling times of each vector species involved. We now give the following definition:

Definition 2. A vector-host mixing probability is called *separable* if and only if

$$p_{ij} = p_i p_j \quad \text{and} \quad q_{ji} = q_j q_i.$$

To obtain separable solutions for our formulas (5) and (6) we require $b_{ij} = b$ for all indices. In this way the contact probabilities become

$$p_j = \frac{m_j}{\sum_{j=1}^n m_j},$$

and

$$q_i = \frac{\tau_i T_i}{1 + b \sum_{k=1}^n \sigma_{ik} m_k} / \sum_{i=1}^m \frac{\tau_i P_i}{1 + b \sum_{k=1}^n \sigma_{ik} m_k}.$$

In this case, the transmission mechanism to susceptible hosts depends on the ratio m_i that measures how the population of hosts is allocated to each vector species.

On the other hand, the transmission mechanism to susceptible vectors depends on the foraging time invested in capturing a host.

4. Applications to food web models

The analysis of community assembly and dynamics has been widely studied both from the experimental as well as theoretical point of view (eg., Cohen et al, 1990; Lawton and Warren, 1988; Hastings and Powell, 1991; Polis, 1991; Paine, 1992). A recent issue of *Ecology* (vol 73(3)) discusses the problem of top-down and bottom-up control in food webs. Hunter and Price (1992) point out that communities are structured by a variety of biotic and abiotic factors acting at all levels of food webs. In this section we model food webs structured through predator prey and consumer resource interactions where predation or consumption rates are frequency-dependent. Each trophic level consists of a finite number of species or types of organisms and the probability that a given prey type is captured and consumed by a predator may be a function of both prey and predator densities. The full description of the approach is given in Velasco-Hernandez and Castillo-Chavez (1992). It derives directly from the modeling of mixing/pair formation processes done by Castillo-Chavez and co-workers (eg., Castillo-Chavez and Busenberg, 1991; Busenberg and Castillo-Chavez, 1991).

Besides allowing omnivory and heterogeneity in prey choice our modeling framework allows for ratio-dependent predator-prey interactions. The use of the mixing/pair formation modelling approach in the context of predator-prey interactions requires the budgeting of prey capture rates for all predator types. The budgeting of rates and the conservation of contacts rate law imply that predator attack rates scale with the ratio of prey to predator numbers. Power (1992), based on the work of Arditi and Ginzburg (1989) and Hanski (1991), argues that ratio dependent models describe interactions where predator interference is important.

4.1 Model formulation

Consider a multi-species community with n species distributed among several prey and predator types. The basic framework of the model is as follows: we let $c_{ij}(t)$ denote the average per capita number of contacts (leading to a successful meal) between a predator of type i and a prey of type j per unit time, while $r_{ji}(t)$ denotes the average per capita number of prey of type j killed and consumed by predators of type i per unit time. Let P_k denote the number or density of species of type k at time t (we do not label differently predators and prey). Then, the conservation property

$$P_i(t)c_{ij}(t) = P_j(t)r_{ji}(t) \quad i > j \quad t \geq 0$$

holds, ie., the total number of prey of type j killed and consumed by predators of type i must equal the number of prey of type j actually captured by predators of type i at all times. We number the species in the community as to reflect their

trophic position in the food web following Cohen et al. (1990). Thus, a given species can predate upon another only if it has a higher number. In a three level food web, for example, top predator, intermediate species and basal prey have the highest, medium, and lowest numbers respectively. Let

$$c_i(t) = \sum_{j=1}^i c_{ij}(t), \quad r_j(t) = \sum_{i=j+1}^n r_{ji}(t)$$

where n is the total number of species in the community.

We define now p_{ij} and q_{ji} for $i > j$ as the proportion of prey of type j on the diet of predator of type i ; and the proportion of the j th prey consumed by the i th predator, respectively. These proportions are given by

$$p_{ij}(t) = \frac{c_{ij}(t)}{c_i(t)}, \quad q_{ji}(t) = \frac{r_{ji}(t)}{r_j(t)}.$$

These proportions satisfy a set of axioms which essentially define them as probabilities with the properties

$$\sum_{k=1}^i p_{ik} = 1 = \sum_{i=k+1}^n q_{ki}$$

and

$$P_i(t)c_i(t)p_{ik}(t) = P_k(t)r_k(t)q_{ki}(t) \quad i > j \quad t \geq 0.$$

If we assume now that predators can switch prey in a frequency dependent fashion making the rate at which prey are killed and consumed a function of predator capture rates. By introducing searching and handling times in the derivation of c_{ij} and r_{ji} , we have shown in Velasco-Hernandez and Castillo-Chavez (1992) that

$$p_{ij} = \frac{b_{ij}P_j}{\sum_{k=1}^i b_{ik}P_k} \quad (7)$$

and

$$q_{ji} = \frac{\frac{\tau_i b_{ij} P_j}{1 + \sum_{k=1}^i \sigma_{ik} b_{ik} P_k}}{\sum_{x=y+1}^n \frac{\tau_x b_{xy} P_y}{1 + \sum_{k=1}^x \sigma_{xk} b_{xk} P_k}}. \quad (8)$$

Expressions (7) and (8) form the basis of our modelling approach. In the next sub-section we present as example the three level food web introduced by Velasco-Hernandez and Castillo-Chavez (1992).

4.2 A three level food web

For clarity of exposition we now relabel the species in the community. We assume that there are n top predator types, m intermediate predator types and l basal prey types. Let N_i , Y_j and T_k denote the basal prey, intermediate predator and top predator respectively. Let $c_i(t)$ and $a_k(t)$ denote the number of prey captured

per unit time by top and intermediate predator respectively; also let $r_k(t)$ and $s_j(t)$ denote the number of individuals of intermediate and basal species captured per unit time by top and intermediate predators respectively.

The conservation relation that must be satisfied is:

$$c_i T_i p_{ik} = r_k Y_k q_{ki}$$

for the top-intermediate level interactions and

$$a_k Y_k \pi_{kj} = s_j N_j \theta_{jk}$$

for the intermediate-basal interactions.

To simplify our model we make the assumption that the contact probabilities depend only on one index, ie., $p_{ij} = p_j$, $q_{ji} = q_i$, $\pi_{xy} = \pi_y$ and $\theta_{yx} = \theta_x$. This type of contact probabilities describe predator prey interactions where contacts are proportionate to the relative numbers of both predator and prey in the community (Velasco-Hernandez and Castillo-Chavez, 1992). Within the original context of the mixing of population these are called *Ross* solutions (eg., Castillo-Chavez and Busenberg, 1991), the simplest kind of interaction that does not assume that predator attack rates scale with the density of prey (the so-called homogeneous predator-prey models). More complex that include a preference component can be formulated.

Let e and b denote the efficiency of capture by top and intermediate predators respectively. These are the parameters that modulate the evolution of the food web since, as Power (1992) points out, the importance of top-down and bottom-up control depends, at least in part, on the efficiency with which consumers exploit their prey. Also let η_i and ρ_j denote the total time allocated to prey search by each intermediate and top predator respectively. Therefore, ω_{ik} is the handling time of intermediate predator i spent on prey of type k ; and σ_{jk} is the handling time of top predator j spent on intermediate prey k . Thus, the time scale of the predation process is introduced as a parameter in this model.

Define $N = \sum_{k=1}^l N_k$, $Y = \sum_{j=1}^m Y_j$, and $T = \sum_{x=1}^n T_x$ as the total number of individuals in each trophic level. The definitions of the contact probabilities are:

$$\begin{aligned} \tilde{p}_j &= \frac{Y_j}{\sum_{k=1}^m Y_k} \\ \tilde{\pi}_j &= \frac{N_j}{\sum_{k=1}^l N_k} \\ \tilde{q}_i &= \frac{\frac{\rho_i T_i}{1 + b \sum_{k=1}^m \sigma_{ik} Y_k}}{\sum_{x=1}^m \left[\frac{\rho_x T_x}{1 + b \sum_{k=1}^m \sigma_{xk} Y_k} \right]} \\ \tilde{\theta}_i &= \frac{\frac{\eta_i Y_i}{1 + e \sum_{k=1}^l \omega_{ik} N_k}}{\sum_{x=1}^l \left[\frac{\eta_x Y_x}{1 + e \sum_{k=1}^l \omega_{xk} N_k} \right]} \end{aligned}$$

The three level food web model is given by the following system of equations. We assume that basal prey in the absence of predation grows in a density-dependent fashion wher \mathcal{K}_k denotes the carrying capacity of the species k .

$$\begin{aligned} N'_k &= r_k N_k \left(1 - \frac{N_k}{\mathcal{K}_k}\right) - s_k N_k \sum_{j=1}^m \theta_{kj} \frac{Y_j}{Y} \\ Y'_j &= \alpha_j Y_j \sum_{k=1}^l s_k \theta_{kj} \frac{N_k}{Y} - r_j Y_j \sum_{i=1}^m q_{ji} \frac{T_i}{T} - \delta_j Y_j \\ T'_i &= \beta_i T_i \sum_{j=1}^m r_j \frac{Y_j}{T} q_{ji} - \delta_i T_i. \end{aligned}$$

Several properties of the model have to be noted. First, the interactions $Y \rightarrow N$ and $T \rightarrow Y$ are typical resource-consumer interactions in which resources are chosen in a frequency-dependent manner with probability θ_j , $j = 1, \dots, l$, and q_i , $i = 1, \dots, m$ respectively. These probabilities are also an indirect measure of the strength of the interaction and indicate, for any given time, how consumers or predators divide their diet among the available resources.

There is a conservation property for food webs derived form the conservation law. In the case of the example being treated here, if we assume that consumers are fully efficient in incorporating biomass of captured prey into their own biomass we obtain

$$T_k \sum_{j=1}^m r_j q_{jk} \frac{N_k}{T} = c_k \frac{T_k}{T} T_k$$

(see Velasco-Hernandez and Castillo-Chavez(1992) for details of the derivation).

The capture rate of prey of a given type depends on the ratio of available prey to total predator density. Since we are assuming that every predator type within a given trophic level shares their diet with every other member of the same predator level, then the likelihood of capturing a prey of, say, type k , depends on the relative demand of that prey type: if the total density of predators is high, this likelihood is small and viceversa. The model thus describes interference competition in a heterogeneous environment (relatively high diversity of resource types, see Hunter and Price, 1992; Power, 1992; Arditi and Ginzburg, 1989).

The model also allows us to keep track of either the individual types within each trophic level or the dynamics of T , Y , and N . The first aspect we call the population dynamics of the web; the second describes directly the *food web dynamics*.

5. Conclusions

We show that the mixing/pair formation approach derived from the study of disease transmission in human populations has wide applicability. The two examples discussed here are intended as illustrative applications. The important fact is the establishment of the conservation of contacts per unit time. This law constraints the time evolution and behavior of the interacting populations. Detailed analytical and numerical studies are needed to evaluate the range of behaviors that are realistic for models formulated under these conditions.

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