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Use of growth functions to describe disease vector population dynamics—Additional assumptions are required and are important

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ABSTRACT

Some important diseases are carried by vectors which can infect susceptible hosts or be infected by infectious hosts. Growth functions may be applied to the vector population. Many growth functions can be constructed from an underlying differential-equation model where birth and mortality processes are identified explicitly. However, this is possible in a variety of ways. The model could be applied to (say) a midge population where infection by a virus is possible when a susceptible midge bites an infectious host, giving rise to incubating and then infectious categories of midge. An infectious midge can then, if biting an uninfected host, infect that host, leading to pathogenic consequences. The submodel used for the vector population partially defines overall disease dynamics, which not only depend on the growth function chosen but also on any extra assumptions about birth and mortality processes which do not affect the growth function per se. The logistic equation is an example of a sigmoidal asymptotic growth function, the asymptote being attained when births and mortality occur at equal rates. Traditionally in the logistic, the interpretation is that birth rate is constant and mortality rate increases as the population increases. A rate function, constant or variable, may be added to both birth and mortality rates without changing total vector population dynamics from the logistic. However, the dynamics of propagation of infection can be substantially different with different assumptions about birth and mortality. This is highly relevant to studies of diseases such as bluetongue in ruminants (involving midges) or dengue in humans (where mosquitoes are involved).

1. Introduction

Arboviral diseases, where the vector carrying the virus to an uninfected host is an arthropod ("arbo" denotes "arthropod-borne"), can exhibit complex dynamics. For example, bluetongue (BT) is a midge-transmitted viral disease of ruminants; the bluetongue virus (BTV) is carried by various species of the biting midge, *Culicoides*. Dengue is a mosquito-transmitted viral disease of humans; here the virus is carried by *Aedes* mosquitoes. Two populations must therefore be considered: hosts, H, and vectors, V, which together determine the overall dynamics of the disease. We have not been able to find a BT modelling publication which makes it clear just how the vector dynamics is treated (e.g. Turner et al., 2012; Sedda et al., 2012). Favier et al. (2005), studying dengue, use modified logistic equations for mosquito dynamics that simulate a logistic; however, they do not discuss the reasons for their particular choice of modification, and neither do they seem to be aware of the other options which are available within the logistic assumption: these can give rise to quite different predictions of the dynamics of infectivity. Similar options and treatments can be used with the Gompertz growth function (in its autonomous time-independent form: e.g. equation 5.29, p. 147, of Thornley and France, 2007) and indeed with other growth functions where growth rate can be written as a sum of positive and negative terms. The logistic function is chosen here to discuss this problem because the logistic is simple and well-known, and continues to be of interest, applicability and further mathematical development (e.g. Thornley and France, 2005; Thornley et al., 2007). In this paper, our objective is to use the logistic formalism as an example of the importance of the underlying assumptions concerning birth and mortality rates; it is shown how the same overall logistic result can be obtained from different assumptions, but that these can give a range of substantially different infectivity dynamics.

2. Modelling

2.1. The basic logistic

The logistic growth equation for vector number, V, can be written by defining the proportional growth rate of V, namely

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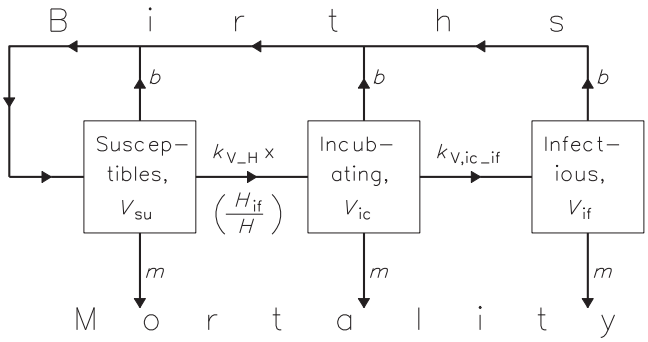

Fig. 1. Vector scheme. The three state variables are shown in the boxes. Rate constants (d^{-1}) are given next to the arrows which denote vector number flow rates (number d^{-1}). See Eqs. (7) for the state-variable differential equations and Table 1 for definitions of symbols, parameter values and units.

$(1/V)dV/dt$, as (e.g. Thornley and France, 2007, pp. 143–145, equation 5.17)

$$\frac{1}{V}\frac{dV}{dt} = \mu_0\left(1 - \frac{V}{V_{max}}\right),$$
$$V(t = 0\,d) = V_0 = 1\ \text{vectors}, \tag{1}$$
$$\mu_0 = 0.2\,d^{-1}, \quad V_{max} = 1000\ \text{vectors}.$$

Here parameter μ_0 (d^{-1}) is the proportional growth rate when $V \to 0$ and V_{max} is the maximum value of V when $(1/V)dV/dt = 0$. The time variable is t (d). Integration of the differential equation leads to

$$V = \frac{V_0 V_{max}}{V_0 + (V_{max} - V_0)\exp(-\mu_0 t)}. \tag{2}$$

This is the familiar logistic growth function, asymptote V_{max}, sigmoidal with an inflexion at $V = V_{inf} = V_{max}/2$ and $t = t_{inf} = \{\log_e[(V_{max}/V_0) - 1]\}/\mu_0$.

Write the first of Eqs. (1) as

$$\frac{1}{V}\frac{dV}{dt} = b - m.$$
$$b = \mu_0, \quad m = \mu_0\frac{V}{V_{max}}. \tag{3}$$

b and m (d^{-1}) can be interpreted as birth and mortality (death) rates. However, it is clear that the birth and mortality rates, b and m, can be supplemented with an arbitrary quantity, μ (d^{-1}):

$$b = \mu_0 + \mu, \quad m = \mu_0\frac{V}{V_{max}} + \mu.$$
$$\frac{1}{V}\frac{dV}{dt} = b - m = \mu_0\left(1 - \frac{V}{V_{max}}\right). \tag{4}$$

The rate variable, μ, may be constant or variable. The logistic equation for V is unchanged although its interpretation may be quite different. Rate variable, μ, could be a function of V, or of the state variables in Fig. 1 below, or, for a non-autonomous system, of time variable t, possibly denoting an environmental dependence. This can lead to different consequences if the logistic is used for disease vector dynamics.

2.2. Disease vector scheme

Next, the scheme in Fig. 1 is applied to a disease vector whose total population V grows according to a logistic. Total population, V, is divided into three classes: susceptible (su), incubating (ic) (infected but not yet infectious) and infectious (if). Note that, although appropriate to this problem, our scheme does not fit exactly into either of the traditional SIR or SEIR epidemiology modelling frameworks (S = susceptible; I = infected and infectious; R = resistant; E = "exposed" = infected but not infectious, i.e. incubating) (e.g. Diekmann and Heesterbeek, 2000, p. 15; Nelson and Masters Williams, 2007, chapter 6). Fig. 1 could be described as an SEI model and lacks a recovered or resistant class, as is considered to be realistic for the vectors (e.g. Lord et al., 1996). Thus (Fig. 1) total population, V, is given by

$$V = V_{su} + V_{ic} + V_{if}. \tag{5}$$

It is also useful to calculate the fractions of V which are susceptible, incubating and infectious:

$$f_{su} = \frac{V_{su}}{V}, \quad f_{ic} = \frac{V_{ic}}{V}, \quad f_{if} = \frac{V_{if}}{V}. \tag{6}$$

With birth rate b (d^{-1}) and mortality rate m (d^{-1}) (Fig. 1), transitions between the susceptible (su), incubating (ic) and infectious (if) classes (Fig. 1) are defined by three differential equations:

$$\frac{dV_{su}}{dt} = b(V_{su} + V_{ic} + V_{if}) - mV_{su} - k_{V\_H}\frac{H_{if}}{H}V_{su},$$
$$\frac{dV_{ic}}{dt} = -mV_{ic} + k_{V\_H}\frac{H_{if}}{H}V_{su} - k_{V,ic\_if}V_{ic},$$
$$\frac{dV_{if}}{dt} = -mV_{if} + k_{V,ic\_if}V_{ic},$$

Adding these and with Eqs. (3), (5) :

$$\frac{dV}{dt} = V(b - m) = \mu_0 V\left(1 - \frac{V}{V_{max}}\right). \tag{7}$$

$$t = 0\,d : V = V_{su} = 1, \quad V_{ic} = V_{if} = 0\ \text{vectors};$$
$$H_{if}(= 10\ \text{say}) \quad \text{and} \quad H(= 100\ \text{say})\ \text{hosts}.$$
$$k_{V\_H} = 1\,d^{-1}, \quad k_{V,ic\_if} = 0.1666^*\,d^{-1},$$
$$c_{V_{max},H} = 10\ \text{vectors per host}.$$
$$V_{max} = c_{V_{max},H}H = 1000\ \text{vectors}.$$

The initial values are for a single vector which is susceptible. All births are susceptible. All classes suffer mortality at the same rate, m. Host numbers are assumed constant, with 10% of total host number H being infectious (H_{if}), although in a larger model these would be variables supplied by interacting vector and host submodels. The biting rate of vectors on hosts, k_{V_H}, is assumed to be the same for all classes of vectors, Fig. 1, and without discrimination between host classes; this term gives the rate at which susceptibles (V_{su}) become infected – fraction H_{if}/H of the hosts are infectious to the feeding vectors, and also the rate at which susceptible hosts become infected (Eq. (8)). The proportional rate at which incubating vectors (V_{ic}) become infectious vectors (V_{if}) is k_{V,ic_if}, giving a mean incubation time of $1/k_{V,ic\_if} = 6$ d. The maximum number of vectors that a host can support is $c_{V_{max},H}$, and hence, with 100 hosts, the asymptote of the logistic, V_{max}, is 1000. It is assumed that infectious vectors, V_{if}, can only die, but cannot otherwise lose their infectivity.

Denote the (input) rate at which susceptible hosts, H_{su}, enter the incubating host class, H_{ic}, I_{Hic}, by

$$I_{Hic} = k_{V\_H}V_{if}\frac{H_{su}}{H}. \tag{8}$$

Here H is the total number of hosts. For constant host numbers, the host infection rate is proportional to V_{if}. It will be seen that the assumptions made concerning birth rate and mortality, with an unchanged logistic for total vector numbers V, can have a substantial impact on the dynamics of host infection.