

## Reply to “Comment on ‘Linking population-level models with growing networks: A class of epidemic models’ ”

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We disagree with Bootsma and Diekmann that our formula for the basic reproduction ratio ( $R_0$ ) has an underlying conceptual mistake. In Phys. Rev. E **72**, 046110 (2005), we propose a large class of growing networks (which we call Kinetic Monte Carlo (KMC) growing networks) as individual-level models for the transmission of infectious diseases. KMC growing networks are conceptually different from the well-established Crump-Mode-Jagers continuous-time branching processes. Thus, the branching process definition of  $R_0$  is not valid for KMC growing networks, and a different implementation of the biological definition of  $R_0$  is necessary.

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Equation (1) in Ref. [2] does not represent our  $R_0$  definition in Ref. [1]. Rather, the right-hand side of Eq. (1) represents what we call  $Q_0$ , the average number of secondary infections over the infectious population. In their Comment [2], Bootsma and Diekmann present the theory of the Crump-Mode-Jagers (CMJ) model as they explicitly specify that a newborn individual lives for an expected amount of time  $1/\mu$  while producing offspring at rate  $\beta$ . In our Kinetic Monte Carlo (KMC) network models,  $\beta$  and  $\mu$  are parameters that describe the population-level dynamics as inflow and outflow of infectious individuals per capita, with no obvious relation to the individual-level processes. That is, in our models,  $\beta$  and  $\mu$  are found by analyzing only population-level data.

Bootsma and Diekmann [2] raise the point that overrepresentation of young individuals in a growing population yields  $R_0=1$ . This is shown in Fig. 4(a) of Ref. [1] that graphs  $R_0$  data from CMJ simulations stratified by date of infection. The average  $R_0$  over all time is 1. However, for early infection times,  $R_0$  approaches  $\beta/\mu$ , while, for later times,  $R_0$  decreases toward zero. This effect is considered a statistical bias in CMJ processes and is called *right censoring*. For the particular CMJ model presented in Ref. [1] each individual is expected to remain infectious for an amount of time  $1/\mu$  infecting  $\beta$  susceptibles per unit time. Thus, they are expected to cause  $\beta/\mu$  secondary infections until their removal; departure of  $R_0$  from  $\beta/\mu$  is considered a statistical bias. Assuming that the transmission of a given disease is accurately described by a CMJ model, contact tracing data can be analyzed to yield  $R_0=\beta/\mu$ . In addition to the method described in Fig. 4(a) of Ref. [1], the average number of secondary infections caused by individuals that are just infected and then followed for their entire infectious period will yield  $R_0=\beta/\mu$  [2]. However, there is a class of KMC

growing networks that have the same population-level expectations as the CMJ model and can be used to analyze the same contact tracing data [1]. These models are based on rules that apply infection and /or removal events to the current state of the disease transmission network. These rules do not define an individual-level scenario that yields an expected  $R_0$  (as for CMJ models). Thus, stratifying  $R_0$  data over the date of infection cannot be interpreted as in the case of CMJ models; for KMC growing networks, right censoring does not occur. Therefore, our  $R_0=1$  result in Sec. III of Ref. [1] is not due to right censoring.

The implementation of the biological  $R_0$  definition in Ref. [1] is different than that in Ref. [2] and it is chosen to reflect the disease transmission network for a much broader model class than CMJ processes. Our definition of  $R_0$  in Ref. [1] is to take the average number of secondary cases over removed individuals as the distribution of secondary cases becomes stationary. This definition has been previously used in data analysis [3] and it does not imply a particular individual-level model; it depends exclusively on the structure of the disease transmission network. A more detailed analysis of the public health impact of our  $R_0$  findings will be given elsewhere [4]. As Bootsma and Diekmann [2] point out, the theory of branching processes is in very good shape. However, to the best of our knowledge, no CMJ model (or any other individual-level for that matter) has yet been fully validated by contact tracing data. Thus, developing individual-level models such as KMC networks that are all compatible with the same population-level data is of particular importance for understanding new potential analysis techniques for contact tracing networks as well as for theoretical modeling. In the future, CMJ and KMC models should be assessed for their biological realism.

[1] R. Breban, R. Vardavas, and S. Blower, Phys. Rev. E **72**, 046110 (2005).

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