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Birth-pulse models of *Wolbachia*-induced cytoplasmic incompatibility in mosquitoes for dengue virus control

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HIGHLIGHTS

- Birth-pulse models concerning the effects of CI on dengue control are proposed.
- Two different density dependent death functions are proposed and considered.
- Strategies of eradicating mosquito and population replacement have been addressed.
- The two strategies can be realized for different death rate functions.

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ABSTRACT

Dengue fever, which affects more than 50 million people a year, is the most important arboviral disease in tropical countries. Mosquitoes are the principal vectors of the dengue virus but some endosymbiotic *Wolbachia* bacteria can stop the mosquitoes from reproducing and so interrupt virus transmission. A birth-pulse model of the spread of *Wolbachia* through a population of mosquitoes, incorporating the effects of cytoplasmic incompatibility (CI) and different density dependent death rate functions, is proposed. Strategies for either eradicating mosquitoes or using population replacement by substituting uninfected mosquitoes with infected ones for dengue virus prevention were modeled. A model with a strong density dependent death function shows that population replacement can be realized if the initial ratio of number of infected to the total number of mosquitoes exceeds a critical value, especially when transmission from mother to offspring is perfect. However, with a weak density dependent death function, population eradication becomes difficult as the system's solutions are sensitive to initial values. Using numerical methods, it was shown that population eradication may be achieved regardless of the infection ratio only when parameters lie in particular regions and the initial density of uninfected is low enough.

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1. Introduction

The vector-borne diseases, dengue fever and dengue hemorrhagic fever, are emerging globally as the most important arboviral diseases currently threatening human populations. More than approximately 50 million people are estimated to be affected by dengue disease each year [1,2]. The dengue virus is transmitted to humans by mosquitoes, especially *Aedes aegypti* and *Aedes albopictus*. As at least four different serotypes of dengue viruses exist, people may be infected with dengue

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more than once [3]. Currently, no specific antiviral therapy or vaccines are available against dengue [4,5], so vector population control remains the principal means of dengue prevention. However, traditional control measures, such as the use of insecticides for reducing mosquito populations are often prohibitively expensive, unsustainable, environmentally undesirable and may lead to insecticide resistance [4]. They are also failing to slow the current dengue pandemic, which has stimulated a search for novel technologies based on genetic manipulation of mosquito vectors to break dengue transmission cycles [6,7].

Wolbachia is a maternally transmitted endosymbiotic bacterium that is estimated to infect up to 65% of insect species and approximately 28% of mosquito species that have been surveyed [8,9]. It lives in the testes and ovaries of its hosts and can interfere with their reproductive mechanisms, inducting a variety of mosquito phenotypes, such as those with cytoplasmic incompatibility (CI), parthenogenesis, feminization of genetic males and so on. Moreover, appearances of these phenotypes depend on the host species and on *Wolbachia* types. The effect of CI causes embryos from females uninfected with *Wolbachia* to die when they are mated with infected males, whereas infected females are not affected in this manner [10,11]. In mosquito vectors, *Wolbachia* induced CI and matrilineal inheritance may have opposite effects, such as population extinction, coexistence or all of the uninfected population may be replaced by infected insects depending on the types of *Wolbachia* involved, the release methods and ratios of infected to uninfected populations. Some *Wolbachia* cannot only successfully spread within mosquito populations through CI but also stop their mosquito hosts from replicating and transmitting dengue virus [12,13]. In addition to mosquitoes, there are many other economically important insects that harbor *Wolbachia* that could be exploited in control measures including *Simulium squamosum*, a vector of onchocerciasis [14], and whiteflies *Bemisia tabaci*, agricultural pests and vectors of plant pathogens [15].

There are two ways to develop *Wolbachia* as a biological control agent against the dengue virus. One is a population suppression strategy whereby a population of mosquito vectors die out in small, pilot, experiments after releases of males infected with *Wolbachia*, such as during the successful suppression of *Culex pipiens* populations in field tests [16,17]. However, male-only releases would not be practical on the scale required for controlling a large area, or for eradication programmes [18]. This is partly because of the danger that females could be released accidentally as a part of a CI strategy that could permit the *Wolbachia* infection type to become established in the host field population. Another strategy shifts from population suppression to replacement by use of CI mechanisms and matrilineal inheritance, which can lead to populations of uninfected mosquitoes being replaced by infected ones, despite releases of only small numbers of the latter [12,13,19,20].

At present, two kinds of mathematical models, involving both discrete-time and continuous-time models, have been investigated for the spread of *Wolbachia* infection [21–27]. The Allee effect and founder control (i.e. one strain survives but another is always driven to extinction) have been demonstrated using a continuous-time model for the behavior of one or two strains of *Wolbachia* within a single well-mixed population. In addition, a discrete spatial model shows patchy persistence of the two strains but it was habitat characteristics rather than space itself that led to persistence [21,22]. Competitions between mutually incompatible strains were studied by [22,24–26]. A more complex outcome of CI in haplodiploid species was reported by [25].

Reproduction of mosquitoes has been assumed to be continuous throughout the year in most models [22,23,26,27]. However, many insects including mosquito populations exhibit what Cauchley [28] termed as a birth pulse growth pattern. Whilst dengue vectors may be at large in some areas throughout the year, where dengue transmission may thus be continuous, in most places both are highly seasonal with the transmission being interrupted. This is the case in China, where no cases occur between January and April before the outbreak season [29]. Dengue vectors have the ability to survive lean periods as eggs, even being able to hatch after periods of desiccation and so new populations emerge afresh at the start of rainy seasons and then give rise to waves of discrete cohorts. Even where the insects may be perennial, their abundances and dengue transmission are highly seasonal with peaks at the height of the rains or shortly after the rainy season. For instance, this is so in Bangladesh [30], India [31–33] and Thailand [34,35]. A female may survive for a couple of months under ideal temperature and moisture conditions. It needs about 12–18 days to go through four separate stages of its life cycle (egg, larva, pupa, and adult) depending on the environment. Here we focus on adult mosquitoes emerging periodically and ignore the details of their morphological transformations during their life cycles. Moreover fertility of mosquitoes is instantaneous in relation to their life span during tropical rainy seasons. For example every female mosquito oviposits two to three times, on average, and produces up to 500 eggs each year before she finally dies [36,37]. So births are seasonal and take place in a relatively short period at each oviposition. Therefore, it is appropriate to replace continuous breeding models with birth pulse models. Such a phenomenon can be well described by impulsive differential equations (hybrid dynamical systems) [38,39], types of equations which are found in almost every domain of the applied sciences [40–42]. The qualitative properties of these systems are embodied in those of equivalent discrete systems which determine the state after a pulse in terms of the state after the previous pulse.

In this study, we investigate an impulsive system at fixed moments with birth-pulse and *Wolbachia*-induced CI in different density dependent death rate functions. The models represent mosquitoes as the principal vectors of dengue virus, with endosymbiotic *Wolbachia* bacteria capable of preventing the mosquitoes from reproducing and transmitting the virus. This can be achieved either by mosquito eradication or population replacement. Firstly, we obtain the stroboscopic maps of impulsive systems with different density dependent death functions. Secondly, for impulsive systems with different density dependent death rates, the qualitative properties of these systems are embodied in those of equivalent stroboscopic systems. However, as it is difficult to study the stability of equilibria for the stroboscopic systems directly, we investigate the existence and stability of equilibria for the systems by their equivalent systems. Moreover, we make some comparisons between original systems and equivalent ones under different density dependent death rate functions. Particularly, there

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