

Evolution and invasion dynamics of multiple infections with *Wolbachia* investigated using matrix based models

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Abstract

Endosymbiotic bacteria are often transmitted vertically from one host generation to the next via oocytes cytoplasm. The generally small number of colonizing bacteria in the oocytes leads to a bottleneck at each generation, resulting in genetic homogenization of the symbiotic population. Nevertheless, in many of the species infected by *Wolbachia* (maternally transmitted bacteria), individuals do sometimes simultaneously harbor several bacterial strains, owing to the fact that *Wolbachia* induces cytoplasmic incompatibility (CI) that maintains multiple infections. CI occurs in crosses in which the male is infected by at least one *Wolbachia* strain that the female lacks, and consequently it favors individuals with the greatest symbiotic diversity. CI results in death of offspring in diploid species. In haplodiploid individuals, unfertilized eggs hatch normally into males and fertilized ones, which would lead to females, either die (female mortality type: FM) or develop into males (male development type: MD). Until now, only one theoretical study, restricted to diploid species, has investigated the associations where multiple CI-inducing *Wolbachia* co-exist, and explored the conditions under which multiple infections can spread. The consequences of double infections on *Wolbachia* maintenance in host populations, and the selective pressures to which it is subjected have not yet been analysed. Here, we have re-written a model previously developed for single infection in matrix form, which allows easy extension to multiple infections and introduction of mutant strains. We show that (i) the CI type has a strong influence on invasiveness and maintenance of multiple infections; (ii) double infection lowers the invasion threshold of less competitive strains that hitch-hike with their companion strain; (iii) when multiple infections occur, as in single infections, the strains selected are those which maximize the production of infected offspring; and (iv) for the MD CI type, invasion of mutant strains can carry the whole infection to extinction.

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1. Introduction

It is generally accepted that vertically transmitted bacteria (i.e., those transmitted from parents to offspring) are selected for low virulence (Frank, 1996; Lipsitch et al., 1996). In fact, symbionts are actually selected for increasing the fitness of their host, and the host/parasite association therefore develops into mutualism, as exemplified by the

evolution of mitochondria from aerobic bacteria to cellular components (Margulis, 1993). Moreover vertical transmission, and especially maternal transmission, usually leads to the genetic homogenization of the symbiotic population present within a single host. At each generation, only a few symbionts colonize the eggs, and this acts as a bottleneck (Mira and Moran, 2002). That is why cases of multiple intraspecific infections are scarce for symbionts.

Do these two observations reflect the outcome of all vertically transmitted symbionts? Reproductive parasitism is an alternative to the outcome of traditional, maternally-transmitted symbiotic associations. These symbionts seldom confer any advantage on their host, and can even inflict a physiological cost on them. Reproductive parasites

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are not rare, since, for instance, bacteria belonging to the genus *Wolbachia* are estimated to infect between 20% and 70% of insect species (Werren and Windsor, 2000; Jeyaprakash and Hoy, 2000), which would make this bacterium the most widespread symbiont within the animal kingdom.

Wolbachia is an endosymbiotic α -proteobacterium that infects many arthropods and nematodes. Although its transmission is essentially maternal via the egg cytoplasm, this bacterium can have a negative impact on the physiology of its host (Min and Benzer, 1997; Fleury et al., 2000). This cost at the individual level is offset at the population level by a relative advantage of infected hosts over uninfected hosts. This advantage is conferred by reproductive manipulations that allow *Wolbachia* to invade host populations, the most common effect being cytoplasmic incompatibility (CI).

In its simplest form, CI is a post-zygotic reproductive isolation that occurs in crosses between uninfected females and infected males (unidirectional CI). CI is caused by an abnormal condensation of the paternal chromosomes, making them unable to participate in karyogamy (Callaini et al., 1997). Depending on the species concerned, CI can result in a variety of outcomes. In diploid species, the incompatible embryos die. In haplodiploid organisms, the situation is more complex. Haploid males resulting from unfertilized eggs develop normally and do not suffer from CI, whereas the females, all of which develop from fertilized eggs, either die as in diploid species (female mortality type, FM; Vavre et al., 2000) or develop into males (male development type, MD; Breeuwer and Werren, 1990).

The epidemiology and evolution of CI-inducing *Wolbachia* have been extensively studied. The advantage conferred on infected females by CI is frequency-dependent. The higher the frequency of infection, the higher the proportion of incompatible crosses for uninfected females. In fact, *Wolbachia* needs to pass beyond a threshold frequency to be maintained and spread into the host population (Turelli, 1994; Vavre et al., 2000). This threshold depends on four parameters: the cost of infection, the efficiency of transmission, the level of incompatibility and the CI type. Moreover, infection can only be maintained over a certain range of parameters (Turelli, 1994; Vavre et al., 2000), and this region of maintenance is greater for diploid species than for haplodiploid ones. In haplodiploid organisms, *Wolbachia* is a more effective invader when the CI is of the FM type than when it is of the MD type (Vavre et al., 2000, 2003).

Studies of selective pressures acting on the host–*Wolbachia* association have concluded that the outcome of competition between two compatible strains is determined by the product of fecundity times transmission, i.e., the number of infected offspring produced by an infected female (Turelli, 1994; Egas et al., 2002; Vavre et al., 2003). The strain that maximizes this product will be the one selected, regardless of the level or type of the incompatibility.

CI also provides an active mechanism for maintaining multiple infections. CI occurs in crosses between individuals

harboring different *Wolbachia* strains (bidirectional CI) (Perrot-Minnot et al., 1996). In other words, CI will be expressed each time a female mates with a male harboring at least one *Wolbachia* that she does not. Consequently, all other things being equal, CI favors females with the greatest bacterial diversity, since this makes them compatible with all the males in the population. Evidence of multiple infections is widespread in the field (e.g. Vavre et al., 1999; Malloch et al., 2000; Jamnongluk et al., 2002; Kondo et al., 2002; Reuter and Keller, 2003), and it is even more common than expected (Werren et al., 1995).

So far, there has been only one theoretical study of the phenomenon of multiple CI-inducing *Wolbachia* infections (Frank, 1998). This study was restricted to diploid species, and focused solely on the dynamics of the double infections. When two strains co-exist within the same host, there are four stable equilibria corresponding either to the loss of both bacteria, to the maintenance of only one or other strain, or to the maintenance of a double infection. Like the threshold found for single infection, Frank (1998) has identified a range of initial frequencies that allow the double infection to be maintained.

Nothing is known about many of the theoretical aspects of multiple CI-inducing *Wolbachia* infection, in particular the selective pressures that act on the association and multiple infections in haplodiploid species have never been studied. This must be done if we are to hope to understand why multiple infections are so widespread. Hitherto, many theoretical studies of *Wolbachia* have been based on the model developed by Turelli (1994) (Frank, 1998; Vavre et al., 2000, 2003; Telschow et al., 2005). To allow us to describe the dynamics of infection with multiple strains over the course of time, we have re-written this model in matrix form and extended it to double infections. This formalism makes it easy to integrate new strains and mutant strains into the population, and to consider the various types of CI. We have used this model to explore the consequences of double infection on *Wolbachia* maintenance in the host populations, and to study the selective pressures acting on *Wolbachia* when multiple infections occur.

2. The matrix model

The model developed here is a Turelli-like model (1994) re-written in matrix form, extended to double infection and integrating the various types of CI. For the sake of clarity, we have used the same notation as Turelli (see below and Table 1). This is a population genetics model in which we are only interested in the changing frequencies of the various types of hosts.

2.1. Re-writing in matrix form

Let us first consider a population harboring only one strain of *Wolbachia*. The change in the frequencies of the various types of host is described by the following

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