# Co-evolution between parthenogenesis-inducing Wolbachia and its hosts.

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# Chapter 8

# General Discussion

I studied the dynamics, causes and consequences of a PI-*Wolbachia* infection in two parasitoid wasps *Tetrastichus coeruleus* and *Asobara japonica.* Interestingly, both species have populations that are infected with *Wolbachia* and reproduce parthenogenetically (thelytoky) and populations that are not infected and reproduce sexually (arrhenotoky) (*T. coeruleus*: chapter 2, Reumer *et al.* 2010; *A. japonica*: Mitsui *et al.* 2007, Kremer *et al.* 2009).

Population genetics shows that different scenarios for the spread of a parthenogenesis-inducing *Wolbachia* infection may occur in different species. A recent study on the PI-*Wolbachia*-infected parasitoid wasp *Leptopilina clavipes*, was the first to show that horizontal transmission of *Wolbachia* plays a major role in the spread of *Wolbachia* between individuals and populations within a novel host (Kraaijeveld *et al.* 2011a, Kremer & Huigens 2011). Although sexual reproduction during the early stages of *Wolbachia* infection may explain the variation in nuclear DNA of *L. clavipes*, it can not explain the variation in mitochondrial DNA (Kraaijeveld *et al.* 2011a, Kremer & Huigens 2011). Similarly, variation in the mitochondrial DNA of *A. japonica* shows that after the initial infection, *Wolbachia* has spread via horizontal transmission (in addition to regular vertical transmission) through the *A. japonica* populations (chapter 6, Reumer *et al.* 2012). I do not have information about the nuclear DNA of *A. japonica.* In contrast, *T. coeruleus* did not exhibit mitochondrial DNA variation, indicating that after the initial infection *Wolbachia* has spread via vertical transmission through the populations and not via horizontal transmission (chapter 3, Reumer *et al.* in prep). Variation in the nuclear DNA of *T. coeruleus* suggests that females mated with males during the early stages of infection, when males were still present, and may still occasionally do so, although males are rare in thelytokous populations (chapter 3, Reumer *et al.* in prep). No variation in *Wolbachia* DNA was found in any of these three parasitoid wasp species (*L. clavipes*: Kraaijeveld *et al.* 2011a; *T. coeruleus*: chapter 2, Reumer *et al.* 2010; *A. japonica*: chapter 7, Kraaijeveld *et al.* 2011b). Therefore, all three species became infected with a single *Wolbachia* strain that has subsequently spread via different mechanisms through the populations of the parasitoid wasps.

Both *T. coeruleus* and *A. japonica* have populations that are infected with *Wolbachia* and populations that are not infected (*T. coeruleus*: chapter 2, Reumer *et al.* 2010; *A. japonica*: Mitsui *et al.* 2007, Kremer *et al.* 2009). The reason for this difference between populations seems to be different for the two species. New bacterial symbiont infections can spread rapidly in host populations. Invasions of *Wolbachia* in *Drosophila simulans* in California and *Rickettsia* (another endosymbiotic bacterium) in *Bemisia tabaci* in Arizona have been reported in which the infection frequency increased from 0% to near fixation in less than 100 generations (Turelli & Hoffmann 1991, Himler *et al.* 2011). However, when host populations occur allopatrically, the spread of a symbiont infection may not be so easy. Similar to *T. coeruleus* and *A. japonica*, the parasitoid wasp *L. clavipes* also has PI-*Wolbachia*-infected and uninfected populations (Pannebakker *et al.* 2004b, Kraaijeveld *et al.* 2011a). Infected populations occur in northern Europe, while uninfected populations occur in Spain. However, no populations were found in the region from the Pyrenees to the Massif Central in France, which seems to act as a geographical barrier preventing gene flow between the infected and uninfected populations (Pannebakker *et al.* 2004b, Kraaijeveld *et al.* 2011a). A geographical barrier also seems to be present between infected and uninfected populations of *A. japonica*. *Wolbachia*-infected populations of *A. japonica* occur on the two Japanese main islands, while uninfected populations occur on the smaller southern islands of Japan (Mitsui *et al.* 2007). The geographical distance between the islands probably is too large for *Wolbachia* to invade the southern islands of Japan (chapter 6, Reumer *et al.* 2012). In contrast, *Wolbachia*-infected and uninfected populations of *T. coeruleus* occur geographically close together within The Netherlands. However, these populations occur in different habitats: *Wolbachia*-infected populations occur in natural dunes areas, while uninfected populations occur on agricultural fields (chapter 2, Reumer *et al.* 2010). Population genetics of *T. coeruleus* shows that there is occasional gene flow from uninfected to infected populations, but not vice versa (chapter 3, Reumer *et al.* in prep). This might explain why the *Wolbachia* infection, until now, never has arrived in the Dutch agricultural fields.

Alternatively, differences between two habitats may select for different *Wolbachia* infection frequencies or reproductive modes. By comparing two populations of *T. coeruleus* that differ in habitat, *Wolbachia* infection and mode of reproduction, I found several differences in life history traits (chapter 4, Reumer *et al.* in prep). An uninfected arrhenotokous population from an agricultural field and a *Wolbachia*-infected thelytokous population from a natural Dutch dune area differed in clutch size, female life span, female weight and female nutrient concentrations. However, in order to determine if and how these life history differences are related to differences in ecology, *Wolbachia* infection or mode of reproduction, life history traits of more populations of *T. coeruleus* should be investigated. This might shed more light on the co-existence of *Wolbachia*-infected and uninfected population of *T. coeruleus* in geographically close proximity.

In most cases of *Wolbachia*-induced parthenogenesis, the infection is fixed and the entire host population consists of females (Huigens & Stouthamer 2003). However, both in *T. coeruleus* and *A. japonica* a small number of male offspring is regularly produced in the otherwise thelytokously reproducing populations (*T. coeruleus*: chapter 2, Reumer *et al.* 2010; *A. japonica*: Mitsui *et al.* 2007, chapter 6, Reumer *et al.* 2012). In *A. japonica*, this male production seems to be a maladaptive side-effect of incomplete co-adaptation between *Wolbachia* and host because of a relatively young *Wolbachia* infection (chapter 6, Reumer *et al.* 2012). In *T. coeruleus*, the *Wolbachia* infection seems to be older than in *A. japonica* (chapter 3, Reumer *et al.* in prep). Therefore, co-adaptation between *Wolbachia* and *T. coeruleus* could evolve over a longer period of time and male production in thelytokous populations of *T. coeruleus* probably has to be explained in a different way.

In *A. japonica*, more than half of the males produced by *Wolbachia*-infected females were also infected with *Wolbachia* (chapter 6, Reumer *et al.* 2012). This was the exact same strain of *Wolbachia* that causes parthenogenesis in females (chapter 7, Kraaijeveld *et al.* 2011b). This PI-*Wolbachia* strain seems to induce vestigial cytoplasmic incompatibility in infected males (chapter 7, Kraaijeveld *et al.* 2011b). In *T. coeruleus*, none of the males from thelytokous populations were infected with *Wolbachia* (chapter 2, Reumer *et al.* 2010).

Apart from the effect a PI-*Wolbachia* strain may have on infected males, it can also have severe consequences for females. In most cases of *Wolbachia*-induced parthenogenesis, the infection is fixed and the entire host population consists of females (Huigens & Stouthamer 2003). In the absence of males and sexual reproduction, genes involved in sexual reproduction are not actively maintained by selection. Accumulation of neutral mutations or selection against the maintenance of costly sexual traits may lead to their loss or deterioration (Carson *et al.* 1982, Pijls *et al.* 1996, Pannebakker *et al.* 2005, Kraaijeveld *et al.* 2009). In addition, females may loose the ability to reproduce sexually due to 'functional virginity mutations' that may spread concomitantly with the *Wolbachia* infection through a population (Stouthamer *et al.* 2010, King & Hurst 2010). Virginity mutations arise during the early stages of PI-*Wolbachia* infection and affect traits in females involved in sexual reproduction, e.g. mating or egg fertilization. Accumulation of neutral mutations or selection against the maintenance of costly traits arise after a longer period of parthenogenetic reproduction and can potentially affect all traits involved in sexual reproduction, e.g. courtship behaviour or pheromone production. Many insect species with female-only populations exhibit deterioration or loss of female sexual traits, such as attractiveness, receptiveness and morphology of sexual organs (Pijls *et al.* 1996, Gottlieb & Zchori-Fein 2001, Kraaijeveld *et al.* 2009). In *T. coeruleus*, I found a longevity cost of mating or sperm storage. Selection against the maintenance of costly sexual traits appears to have resulted in the degradation of receptivity and spermathecal morphology of thelytokous females (chapter 4, Reumer *et al.* in prep). However, arrhenotokous and thelytokous females were equally attractive to males. Although thelytokous *T. coeruleus* females never mated in the lab, I found clues for occasional matings between males and thelytokous females in the field (chapter 3, Reumer *et al.* in prep). Because of these sporadic matings, females may still be exposed to costs of mating due to male manipulations and adaptations of females against these manipulations keep evolving. However, I cannot exclude that these traits (also) have degraded due to functional virginity mutations or accumulation of neutral mutations. In *A. japonica*, females from thelytokous populations that were cured from their *Wolbachia* infection with antibiotics were not capable of sexual reproduction (Kremer *et al.* 2009). Moreover, *A. japonica* males never exhibited courtship towards thelytokous females; thelytokous females were not attractive to males. Because the *Wolbachia* infection in *A. japonica* seems to be relatively young, these traits may have degraded due to functional virginity mutations or strong selection against the maintenance of costly traits, rather than accumulation of neutral mutations.

The comparison of populations that are infected with parthenogenesis-inducing *Wolbachia* and thus reproduce asexually and populations that are not infected and thus reproduce sexually, increases the understanding of the evolution of sexual reproduction. The consequences of asexual reproduction at a genetical and phenotypical level can be studied by comparing individuals from PI-*Wolbachia*-infected and uninfected populations. In addition, the traits that are involved in sexual reproduction and the rates at which these traits deteriorate and are lost can be studied by comparing different species that differ in the age of their PI-*Wolbachia* infection.

Absence of migration and gene flow between *Wolbachia*-infected and uninfected populations because of geographical or ecological boundaries, together with the ongoing co-evolution between *Wolbachia* and host, and deterioration and/or loss of genes that are no longer used, may lead to larger differences between populations. In theory, these differences may eventually lead to speciation between *Wolbachia*-infected and uninfected populations.