Wolbachia [1]

By: Prevot, Karine Keywords: Marshall Hertig [2]

Bacteria of the genus *Wolbachia* [3] are bacteria that live within the cells of their hosts. They infect a wide range of arthropods (insects [4], arachnids, and crustaceans) and some nematodes (parasitic roundworms). Scientists estimate that *Wolbachia* exist in between seventeen percent and seventy-six percent of arthropods and nematodes. The frequency of the bacteria makes them one of the most widespread parasites. In general, they are divided into five groups, from A to E, depending of the species of their host. They cause diverse reproductive and developmental changes on their numerous invertebrate hosts. Several mechanisms, like the feminization of the embryo's sexual characters, are involved in those processes. To reproduce, *Wolbachia* often exploit their hosts' reproductive processes. Additionally, they are symbiotic in that they are necessary for the normal development of organisms in some species.

In 1924, Marshall Hertig in Minneapolis, Minnesota, and Simeon Burt Wolbach at Harvard University [5] Medical School in Boston, Massachusetts, first described *Wolbachia* in the mosquito *Culex pipientis* [6]. They studied micro-organisms called Rickettsiae, which are intracellular parasitic bacteria that are widespread among arthropods. To do so, they examined several arthropods, including twenty-five males and females of *Culex Pipens* mosquitos collected near Boston and near Minneapolis. They observed intracellular organisms that only infected the ovaries and testes [7], and that were also found in the eggs. In 1936, Hertig named these particular parasites *Wolbachia pipientis* [8].

In the 1950s, Hannes Laven, from the Institut für Genetik of Johannes Gutenberg-University in Mainz, Germany, discovered that some *Culex Pipens* mosquitos failed to breed with others from the same species, even when forced to in experiments, producing few or no progeny. Laven established that a incompatibility factor transmitted from parents to offspring through females only, and he named this phenomenon cytoplasmic incompatibility. In 1971, Janice Yen and Ralph Barr at the University of California in Los Angeles, California, found that mosquito eggs were killed when the sperm [9] of males infected by *Wolbachia* fertilized non-infected eggs. In 1990, Richard Stouthamer at the University of California in Riverside, California, found that *Wolbachia* could make males dispensable for reproduction in some species, by feminizing the population and producing parthenogenesis, a process of reproduction that does not involve fertilization [10]. Researchers began to study *Wolbachia* with molecular methods like polymerase chain reaction (PCR), a biochemical technology used to generate copies of a particular DNA sequence, and that enabled researchers to detect and to identify the bacteria more easily and rapidly.

In his 1936 article, Hertig had showed that bacteria could transmit from one organism to another in two ways. Most often, they pass from mother to the offspring through the egg [11] cytoplasm. However, there are few exceptions. In some cases, bacteria transmit from one individual to another, even across species, regardless of reproduction. In all cases, the transmission increases the number of bacteria and, for the infected population, results in a biased sex-ratio, in which the number of females in the population exceeds the number of males. These bacteria can infect many different types of organs. Most notably, they infect the testes [7] or ovaries of their hosts. *Wolbachia* are present in mature eggs, but not in mature sperm [9], so when bacteria are present in males, they are eliminated from the germ-line during spermatogenesis. Therefore, only infected females pass the infection to their offspring.

Wolbachia alter both reproduction and development of their hosts. There are several ways and several mechanisms by which those alterations happen. In some cases, the symbiosis is considered to be facultative, which means that if the bacteria are removed, such as with antibiotics in a laboratory, the hosts can still reproduce and develop normally. In other cases, the symbiosis is considered obligatory, which means that the bacteria are necessary for the hosts to reproduce and develop normally. In facultative symbiosis, there are four main altered phenotypes that are possible: feminization, parthenogenesis, male-killing, and cytoplasmic incompatibility.

Feminization, a process by which geneticly male organisms turn into females, characterizes the infections of male organisms by *Wolbachia*, which require females to reproduce and survive. In the 1990s, Thierry Rigaud and his collegues at the University of Poitiers in Poitiers, France, studied this phenomenon in crustaceans. In crustaceans with female heterogamety, males have ZZ sexual chromosomes and females have ZW sexual chromosomes, similar to how human males have XY sexual chromosomes and human females XX sexual chromosomes. *Wolbachia* turn genetic males into functional females able to reproduce and produce offspring despite their genetic sex (ZZ). *Wolbachia* inhibits the production of androgen hormones [12] that are responsible for the development of males' sexual characters, making the gonads develop female characters instead. Feminization may depend on endocrine-related processes, such as hormonal variations.

As *Wolbachia* do not infect a whole population of hosts, some males remain in the population. However, Rigaud and his research team suggested that *Wolbachia* that feminize males can influence the evolution [13] of crustaceans by leading to a complete loss of female heterogamety. Several populations of the common pill-bug *Armadillidium vulgare* [14] no longer have

females with a ZW sex chromosome. These females are in fact genetic males, which *Wolbachia* turned into females. Feminization then leads to a sex-ratio of the host population that favors females.

The second way that *Wolbachia* alter their hosts is to cause them to reproduce via parthenogenesis. Parthenogenesis [15] is a form of reproduction without fertilization [10] in which eggs can grow and develop into embryos and eventually into adults. In 1990, Richard Stouthamer and his colleagues at the University of Rochester in Rochester, New York, studied parthenogenesis in wasps. In some parasitic wasps and acari, fertilized eggs contain two pairs of chromosomes (they are diploid) and usually develop into females, whereas non-fertilized eggs contain only one copy of each chromosome (they are haploid) and develop into males. When *Wolbachia* infect haploid egg [11] cells, they double the haploid set of maternal chromosomes in the egg [11], causing the eggs to develop into females. Infected females can produce twice as many offspring as the non-infected ones. Thus the bacteria alter how their hosts reproduce and develop so that the bacteria can better spread in their hosts' populations.

The other two phenotypes induced by facultative symbiosis are male-killing (death of males), and cytoplasmic incompatibility (incompatibility between sperm [9] and egg [11]). In those two processes, *Wolbachia* induce developmental and reproductive variations in their hosts. In 1999, Gregory Hurst and his colleagues at the University College London [16] in London, UK, showed that male-killing *Wolbachia* infect the ladybug *Adalia bipunctata* [17] and the butterfly [18] *Acraea encedon* [19] and cause the male embryos to die. As the two species have different reproductive mechanisms, Hurst and his colleagues hypothesized that *Wolbachia* also evolved different mechanisms to recognize a host's sex.

Cytoplasmic incompatibility, as Laven had described in 1967, is an incompatibility between sperm [9] and egg [11], for which *Wolbachia* is responsible. This incompatibility silences the paternal chromosomes of infected embryos. In the infected organisms, the infected eggs often die. In 1990, Johannes Breeuwer and John Werren of the University of Rochester in Rochester, New York, described two kinds of cytoplasmic incompatibility: unidirectional and bidirectional. Cytoplasmic incompatibility is often unidirectional. When infected males mate with uninfected females, they fail to produce viable [20] offspring, whereas when uninfected males mate with infected females, they can produce viable [20] offspring. Bi-directional incompatibility occurs when different and incompatible *Wolbachia* strains infect males and females, and when those infected males and females mate with each other, they fail to produce viable [20] offspring. In all cases, cytoplasmic incompatibility results from an abnormal condensation of paternal chromosomes in the fertilized egg [21], which prevent paternal chromosomes from contributing to the development of the egg [11].

Wolbachia infections that cause incompatibility can spread rapidly through a population, as infected eggs are compatible with both infected and uninfected sperm [9] whereas uninfected eggs are only compatible with uninfected sperm [9]. These infections can influence the evolution [13] of a population such that all females in the population become infected. The processes of infection, especially male-killing, can indicate emerging selection pressures at the community-level. The populations of infected ladybugs, for example, produce cannibal larvae that eat mostly other larvae. There is a strong competition for survival between larvae. In this context, dead male larvae provide a source of food for the female larvae that eat still-born males. This phenomenon decreases the level of antagonistic interactions between siblings and favors the development of female larvae.

These four phenotypes suggest that external factors like bacteria can control the processes of reproduction and development of a host. Host populations are manipulated and altered in such a way that *Wolbachia* can be more important than the hosts' genes [22] to the determination [23] and the development of sex characteristics. But beside these four phenotypes, *Wolbachia* are also responsible for obligatory symbiosis, in which the hosts cannot develop without the bacteria.

In 2001, Frank Dedeine and his colleagues at the University of Lyon 1 in Lyon, France, found that without *Wolbachia*, female wasps of the species *Asobara tabida* [24] failed to produce egg [11] cells. Three different strains of *Wolbachia* infected those wasps. Two of them induced incompatibility between sperm [9] and eggs, resulting in no progeny, whereas one was involved in oogenesis. When Dedeine and his research team used antibiotics to kill *Wolbachia* in the female wasps, the wasps failed to produce mature egg [11] cells, and thus could not reproduce. The research team hypothesized that this phenomena resulted from a long co-evolution [13] between the wasps and *Wolbachia*, in which the hosts have become dependent on *Wolbachia*. Dedeine and his colleagues suggested that the wasp species or its ancestors became associated with a strain of the bacteria necessary to produce egg [11] cells. This association would have led to a functional redundancy of host and symbiotic genes [22]. Because there is no need to have two genes [22] with the same function, the occurrence of functional redundancy can lead to the loss of function of genes [22] in one of the symbiont. In this case, the host itself lost the capacity to produce the function, becoming totally dependent on *Wolbachia* for reproduction and development.

In some nematode worms [25], *Wolbachia* are also necessary for normal development and fertility. Filarial nematodes are parasites of the tropics, and are responsible for human diseases like onchocerciasis, called river blindness, or elephantiasis, characterized by the gross enlargement of body parts. In 2003, Achim Hoerauf and his colleagues at the Rheinische Friedrich-Wilhelms-University of Bonn [26] in Bonn, Germany, suggested that because elimination of *Wolbachia* from filarial nematodes results in either death or sterility of the nematode, an antibiotic treatment to remove the bacteria could control filarial nematode diseases.

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Subject

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Topic

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