A WAY OF REPRODUCTIVE MANIPULATION AND BIOLOGY OF *Wolbachia pipientis*

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ABSTRACT

The endo-symbiotic relationship between microorganism and eukaryotes are very common and has been broadly investigated from all insect species. The genus *Wolbachia* are obligatory intracellular bacteria that induce evolutionary alterations and have been frequently reported in egg cytoplasm's of various invertebrates including insects, spiders, mites, scorpions, crustaceans and nematodes, which exert a profound impact on host biology and behavior through a number of phenotypic alternations. Due to its ubiquitous phenotypic behavior, *Wolbachia* becomes a novel and promising natural micro-biocontrol agent to induce cytoplasmic incompatibility, killing of male embryos, parthenogenesis, and feminization. Autonomous transgenic capability, survival on several host species and the ability to modify the host reproductive systems makes it the most prominent and focusing scientific genomic research from last few decades. The aim of this review is to summarize the significance and recent discoveries of *Wolbachia* related to various arthropods which lead positive directions to be exploited in future for integrated pest management (IPM) strategies. Further, this review also discussed the biology, phylogeny, distributions, classifications and types of *Wolbachia* infections on insect orders and coleopterans in particular.

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1 Introduction

Wolbachia pipientis are maternally inherited gram negative bacteria which becomes a potential endo-symbiotic microbial biocontrol agent (Jeong & Suh, 2008). It belong to order Rickettsia and are reported in the cytoplasm of various insects (Jeong & Suh, 2008), terrestrial nematodes (Bourtzis & Miller, 2003), crustaceans (Cordaux et al., 2012) and Arachnid (scorpions) (Baradaran et al., 2014; Bryson, 2014). From last few years *Wolbachia* gained much attention and extensively used against various pest and vector management (Xi & Dobson, 2005) through manipulating the targeted reproductive system, interference with nutritive and metabolic pathways, distortions the biology of host by various infectious phenotypes like incompatibility of cytoplasm (CI), killing of male embryos, parthenogenesis and feminization (developing the female characters into male) (Anbutsu & Fukatsu, 2010). These autonomous infectious mechanisms support reproductive phenomenon of the infectious organism and allow the *Wolbachia* to increase their infection.

Various theoretical and empirical studies suggest that among available alpha-proteobacteria, *W. pipientis* is more prominent and effective transmitter of intracellular symbiotic infections which known to infect more than 2/3 of global insect communities (Hilgenboecker et al., 2008) ranging from 20 - 76% (Tagami & Miura, 2004). Moreover, some species of class insecta (lice, Anoplura: Mallophaga) also had 100% *Wolbachia* infections (KYEI-POKU et al., 2005).

Wolbachia, not only known as inhibitor of reproductive systems but also known to direct distinguish effect on reduction the diverseness of mtDNA (Galtier et al., 2009). Although, some contradictory views also existed about the effects of *Wolbachia* and diversity in nuclear material (Telschow et al., 2002), this is because *Wolbachia* and mtDNA are both transmitted via mother offspring's and hypothesized that reducing the diversity of mtDNA hitches beside as increasing of *Wolbachia* infections (Armbruster et al., 2003).

Most of the earlier researchers and biologists believed that *Wolbachia* is maternally inheritable symbionts, i.e. only vertically transfer from egg cytoplasm to offsprings. However recent studies indicate that *Wolbachia* could also cause infection through horizontal transfer from infected uninfected species (Kawai et al., 2009). It can also be cultured outside the cell (Rasgon et al., 2006) that have great potential to transfer infection and live outside the host cell (culture cell) over a reasonable period of time (Dobson et al., 2002b). This discovery of *in vitro* production of *Wolbachia* leads researcher towards positive direction and not only open the doors of IPM programs in agriculture sector but also help to control the insect vector of various human disease i.e. Dengue, Chikungunya, and Plasmodium (Moreira et al., 2009)

Over the last few decades, *Wolbachia*-arthropods association becomes a focusing research point and attract intense

fascination of researchers and genomic scientists due to its multiple behaviors, diverse host range, potential for rapid host speciation and have a great ability to alter host embryonic progress and mitotic developments (Lassy & Karr, 1996). It has also great potential to control the population of insect's pests as a microbial natural enemy with multiple ways of infectious phenotypes to manipulate host biology of targeted populations. Due to its ubiquitous behaviors, evolutionary, biologically and ecologically it has become a key potential intracellular biocontrol agent in pest biocontrol strategies. This review highlights and evaluates updated genetical, biological and ecological role of *Wolbachia* in various insect orders which can be used as the potential role in future integrated pest management (IPM) strategies.

2 Taxonomic characteristics of the *Wolbachia*

Wolbachia species are members of the obligate intracellular Rickettsiales and forge as a dual competitive microbial agent (DCMA) like parasitic relationships with numbers of arthropods and mutualistic relationships with various insect orders, particularly with nematodes. During their 100-million-year interaction with their hosts, the cytoplasmic transmitted bacteria have evolved as "reproductive parasites which belongs to Class: Alpha-proteobacteria, order Rickettsiales and Family Rickettsiaceae, firstly reported by entomologist, Marshall Hertig and Samuel Wolbach in 1924 from sex cells of *Culex pipiens* Linnaeus (mosquito) (Hertig & Wolbach, 1924). However, comprehensive publication was done in 1936 (Hertig, 1936).

3 Phylogeny and Classification of *Wolbachia*

Among the family Anaplasmataceae, *Wolbachia* is well known for its capacity to alter the reproductive developments of host (ovaries and testes). It is considered as most common endosymbiotic bacteria that infect millions of insect species from all around the globe (Jeyaprakash & Hoy, 2000; Hilgenboecker et al., 2008). Within the class of alpha-proteobacteria, *Wolbachia* also has members such as *Anaplasma*, *Ehrlichia*, *Neorickettsia* which are genetically much-closed genera to *Wolbachia* (Figure 1 (a)).

On the basis of sequence information obtained with targeted bacterial genes includes 16S rDNA (partial small subunit ribosomal DNA, *groEl* (heat shock protein gene), *wsp* (outer surface coat protein gene) (Baldo et al., 2006; Paraskevopoulos et al., 2006) and *ftsZ* (cell division gene), *Wolbachia* infections have been characterized and divided into eight super groups A-H (Zhou et al., 1998; Bordenstein et al., 2009; Ros et al., 2009). Moreover, some recent literature reported that infectious strains of *Wolbachia* can further be classified into 3 more super groups, that's A-K super orders (Zhou et al., 1998; Bordenstein et al., 2009; Ros et al., 2009; Salunke et al., 2010) as shown in Figure b (1): Table. 1.

Figure 1 (a) Division of *Wolbachia* with genetically closed genera within class alpha-proteobacteria: (b) Division of *Wolbachia* strain into 11 super groups within different host species.

4 Identification and detection of *Wolbachia*

Wolbachia is completely dependent on the cytoplasmic atmosphere of the host. The average size of these bacteria is ranging from 0.8 to 1.5 μm (Herting et al., 1936) and covers by at least 2 cell membrane. Although these bacteria have been identified as maternally inherited infection through infected mother to offspring's but the infections of *Wolbachia* is not only limited to reproductive systems of the host but it also infect and colonized in various tissues such as muscle cell, digestive organs, brain, fat body and hemolymph of the host (Min & Benzer, 1997; Cheng & Aksoy, 1999; Dobson et al., 1999; Cheng et al., 2000; Serbus et al., 2008; Albertson et al., 2009). Infection of *Wolbachia* can be confirmed within the tissues of various invertebrates by using various identification techniques such as visualized Giemsa stain (Herting et al., 1936), fluorescent dye DAPI, fluorescent cells nucleic acids dye SYTO 11 techniques (Albertson et al., 2009). Furthermore, in situ hybridization with specific *Wolbachia* DNA probes and staining of immune through antibodies (Moreira et al., 2009) is also used for the diagnosing the *Wolbachia* infection inside the host tissues. A very sensitive PCR (Polymerase chain reaction) technique along with other tools like Hybridization of DNA and analysis of sequence are also extensively used for *Wolbachia* detection.

Table 1 Division of *Wolbachia* infections into 11 supergroups

Super-groups	Host name	References index
A, B, E	Arthropods	(Vandekerckhove et al., 1999; Lo et al., 2002; Lo et al., 2007)
C, D	Filial Nematodes	(Lo et al., 2007)
F	Both Arthropods and Nematodes	(Campbell et al., 1992; Rasgon & Scott, 2004)
G	Spiders	(Goodacre et al., 2006)
H	Termites	(Bordenstein et al., 2009)
I	Siphonaptera	(Ros et al., 2009)
J	Spirurida, Nematoda	(Ros et al., 2009)
K	Prostigmata, Acarina	(Ros et al., 2009)

Table 2 Killing of male embryo discovered into following host species.

Host name	References
Coleoptera	(Majerus & Zakharov, 2000)
Diptera	(Dyer & Jaenike, 2004)
Lepidoptera	(Jiggins et al., 1998; Jiggins et al., 2000; Fujii et al., 2001; Jiggins et al., 2001)
Class Arachnida	(Zeh et al., 2005; Koop et al., 2009)

5 *Wolbachia*-host association

The endosymbiont *Wolbachia* manipulate and alter the host reproductive systems (Werren et al., 2008) through various phenotypic mechanisms such as the killing of male sperm, feminization, cytoplasmic incompatibility and parthenogenesis. All phenotypes are focus on the enhancing the progenies of infected female of associated host population and therefore, may cause the reason to increase the transmission and availability of bacteria within the hosts. These effects may be beneficial or detrimental, and are confounded by genetic and environmental factors. Our focus is to enlighten the host-interactions with most recent investigation related to insect communities by following phenotypic behaviors.

5.1 Killing of male embryos

Wolbachia is one of several types of maternally-inherited bacteria that kill males during embryonic development (Stevens et al., 2001) and significantly reduced the populations of males. Hence, infected females may lay a mixed brood of male and female eggs, but only female eggs survive to become adults. A broad range of endosymbionts like *Flavobacteria*, *Rickettsia*, *Arsenophonus*, *Wolbachia*, and *Spiroplasma* are associated with the host and responsible for induction of male killing (Anbutsu & Fukatsu, 2010) but cytological mechanisms causing male-killing are still unknown (Hornett et al., 2006; Sheeley & McAllister, 2009). Killing of a male reported in class Insecta including Lepidoptera, Diptera and Coleoptera and class Arachnid (Table 2).

5.2 Feminization

Feminizing strains of *Wolbachia* make changes in genetic of male hosts and force it to develop into functional female which is known as alteration of sex or feminization. Such infections are common in terrestrial isopods especially in woodlouse, *Armadillidium vulgare* have been best studied (Rousset et al.,

1992; Cordaux et al., 2012). Sex in these crustaceans is determined by the action of a male hormone that suppresses female development. *Wolbachia* is thought to inhibit development of the androgenic gland that produces this hormone and also may block receptor sites required for hormone activity. It is one of the most advantageous mechanisms of *Wolbachia* in which double offspring of the female which eventually increase the rate of infections. So far, the limits of *Wolbachia* distribution via feminization have been discovered only in three orders of class Insecta (Table 3) and yet needs to be determined more.

5.3 Cytoplasmic incompatibility

Cytoplasmic incompatibility (CI) is the most abundant *Wolbachia* induced phenomena that alter the host reproduction. The presence of CI in *Wolbachia* have been frequently reported in wide range of insects includes flour beetles, alfalfa weevils, wasps, plant hoppers, fruit flies, flour moths, wood louse, mites and numerous mosquitoes species.

CI may occurred by matting's between *Wolbachia* infected males and uninfected females, or between any partners infected with different strains of *Wolbachia*. However, CI occurs in two directions; when *Wolbachia*-infected male cross with uninfected female causing unidirectional CI. Secondly when both male and female carry opposite strains which are contrastive to each other known as bidirectional CI (Telschow et al., 2005; Merçot & Poinot, 2009). These types of CI caused higher embryonic death and organism produced less number of progenies (Breeuwer & Werren, 1990; O'Neill & Karr, 1990; Bourtzis & O'Neill, 1998; Breeuwer & Werren, 2007; Bourtzis & Miller, 2014). Recently Tram et al. (2003) reported the occurrence of *Wolbachia* in male sperm and found that it introduces a factor here that prevents embryogenesis in the fertilized egg, unless the female partner is infected with the same *Wolbachia* strain to allow the sperm's 'rescue'.

Table3 Feminization identified into different hosts.

Host name	References
Lepidoptera	(Hiroki et al., 2002; Kageyama et al., 2002; Narita et al., 2007)
Hemiptera	(Negri et al., 2006)
Terrestrial Isopods	(Verne et al., 2007; Bouchon et al., 2008)

Table 4 Cytoplasmic incompatibility identified into different host.

Host name	References
Coleoptera	(Stevens & Wade, 1990)
Diptera	(Yamada et al., 2011; Zheng et al., 2011)
Isopods	(Moret et al., 2001)
Acari	(Zhang et al., 2015)
Lepidoptera	(Brower, 1976; Kellen et al., 1981)
Hymenoptera	(Reed & Werren, 1995)
Homoptera	(Noda, 1987)

Table 5 Discoveries of induction of parthenogenesis into different host.

Host name	References
Thysanoptera	(Arakaki et al., 2001)
Acari	(Husseneder & Collier, 2009)
Hymenoptera	(Pannebakker et al., 2005)

Unidirectional CI is most frequent and usually occurs between males infected with a single strain or female without any strain of *Wolbachia*. While the bidirectional CI have been reported only in the condition when both partners are infected with the same *Wolbachia* strains. The reason of wide spreading this phenotype because of two elements responsible for two different *Wolbachia* antagonistic functions (Werren, 1997; Poinso et al., 2003) known as modification and rescue. Like other phenomena, CI also have limited investigations in various *Wolbachia* associated hosts (Yamada et al., 2007). Therefore it is necessary to investigate this phenotype in all insect communities. The most recent discoveries of CI induced by *Wolbachia* are given below in Table 4.

5.4 Induction of parthenogenesis

Wolbachia also associated with parthenogenesis induction (PI) in different host species. Offspring's of these insects have three different types of sex determination i.e. diploid male and female (diplodiploidy); haploid male and diploid female (haplodiploidy); diploid female without a male (thelytoky) (Normark, 2003). *Wolbachia* increases the targeted infected female offspring by second type (haplodiploid) of sex determination in various insect species. PI bacteria are found in both A and B divisions of *Wolbachia*, and phylogenetic evidence suggests that PI has evolved several times independently in these bacteria. It therefore appears that PI can evolve easily in the *Wolbachia*. Still lot of work needs to be done to determine, how PI *Wolbachia* cause gamete duplications, disruption of the centrosome or spindle formation, attachment of the spindle to the chromosomes, or spindle kinetics. So far, reported discoveries of *Wolbachia* via PI in various arthropods are discussed below in Table 5.

6 Parasitic role of *Wolbachia*

Wolbachia (Rickettsiales: Rickettsiaceae) are one of most active maternally inherited endosymbiotic proteobacteria that

inhabit wide range of arthropods and nematodes to manipulate their reproductive systems. Parasitic behavior of intercellular bacteria with invertebrates are very common and play an important role to manipulate host biological interactions such as reproductions, developments, gene expression (Zhao et al., 2013) and immune systems (Ivanov & Littman, 2011). A bulk of researches have been conducted to identified the insect-bacteria association particularly *Wolbachia* exerts negative impacts to reduce host fitness, responsible for degradation and early death (Min & Benzer, 1997), responsible for pathogen dissemination (Cook et al., 2008), reduce host survival rate (McMeniman et al., 2009), manipulate reproductive system (McGraw et al., 2001) and inhibit the pathogenicity of host (Walker et al., 2011). With these above reproductive manipulations, the bacterium (*Wolbachia*) thrives in its various hosts at the expense of the hosts' reproduction and act like reproductive parasite to reduced host populations successfully.

7 Mutualistic role of *Wolbachia*

Endo-symbiotic microorganism, particularly *Wolbachia* are not only played an important role in manipulating of host reproduction but also provide protection against targeted host pathogens (Moran et al., 2008; Gross et al., 2009; Cook & McGraw, 2010). It is beneficial for the host species (Taylor et al., 2013) by increasing the survival rate of host or insect species (Vala et al., 2003; Dobson et al., 2004; Foster et al., 2005; Weeks et al., 2007; Zhao et al., 2013) or enhancing the fecundity rate (Girin & Bouletreau, 1995; Dobson et al., 2002a; Fry et al., 2004; Xie et al., 2011). In *Tribolium confusum* (Coleoptera: Tenebrionidae) infected male sperm with *Wolbachia* takes long reproductive time than compared to uninfected ones. Infection may also result to protect the host by suppressing the harmful genes (*Drosophila melanogaster*) (Starr & Cline, 2002; Clark et al., 2005). Moreover in *Tetranychus urticae*, *Wolbachia* also causes interference in the metabolism of iron which decreases oxidative stress and reduces the death of cells, eventually, enhance the chance of

reproduction within the host (Kremer et al., 2009). Another mutualistic example of *Wolbachia* is in wasp, *Asobara tabida* (Dedeine et al., 2005) here it is very essential for embryogenesis, it also play a hypothesised role in ferritin expression (Kremer et al., 2009; Kremer et al., 2012), in fruits flies, *D. melanogaster*, *D. simulans* it caused resistance against viral RNA infection (Hedges et al., 2008; Teixeira et al., 2008; Osborne et al., 2009), in mosquitoes, *Aedes aegypti* it activate the immune systems against numerous pathogens (Moreira et al., 2009; Bian et al., 2010; Van den Hurk et al., 2012) and are also responsible for the microRNAs expressions (Hussain et al., 2011).

8 *Wolbachia* discoveries in Order Coleoptera

Order Coleoptera economically and ecologically recognized has a big and successful order cover almost 1/4 of all known animals species (Hunt et al., 2007). The intercellular relationships with microorganism are very common and frequently investigated in many species of arthropods. Some endosymbionts are very important and play a significant role in development and survival of the various hosts. Last few decades members of class alpha-proteobacteria particularly *Wolbachia* are widely identified in numerous species of order Coleoptera and more than thirty (30) beetle species have been discovered in this intracellular bacteria so far (Lachowska et al., 2010) and all belong to supergroups A and B, except *Rhinocyllus conicus* (Froehlich) which belongs to supergroup F (Lo et al., 2002) (Table 6).

Table 6 *Wolbachia* discoveries in coleopteran species.

Common name of weevil	Scientific name	Family	References
Azuki bean beetle	<i>Callosobruchus Chinensis</i>	Bruchidae	(Kondo et al., 1999)
Vine weevil	<i>Otioryhynchus sulcatus</i>	Curculionidae	(Son et al., 2008)
Ladybird beetle	<i>Adalia bipunctata</i> L.	Coccinellidae	(Sokolova et al., 2002; Elnagdy et al., 2013)
Two spotted Ladybug	<i>Adalia bipunctata</i>	Coccinellidae	(Hurst et al., 1992)
Flour beetle	<i>Tribolium confusum</i>	Tenebrionidae	(Wade & Stevens, 1985)
Black flour beetle	<i>Tribolium madens</i>	Tenebrionidae	(Fialho & Stevens, 2000)
Bark beetle	<i>Pityogenes chalcographus</i>	Scolytinae	(Wolfgang et al., 2009)
Rice water weevil	<i>Lissorhoptrus oryzophilus</i> Kuschel	Curculionidae	(Chen et al., 2012)
Raspberry beetle	<i>Byturus tomentosus</i>	Byturidae	(Malloch et al., 2000)
Tribe naupactini		Curculionidae	(Rodriguero et al., 2010)
Alnus ambrosia beetle	<i>Xylosandrus germanus</i>	Curculionidae	(Kawasaki et al., 2010)
Northern Corn rootworm	<i>Diabrotica barberi</i>	Chrysomelidae	(Roehrdanz & Levine, 2007)
Bean beetles	<i>Callosobruchus Chinensis</i>	Chrysomelidae/ Bruchinae	(Kondo et al., 2011)
Cabbage Seedpod weevil	<i>Ceutorhynchus obstrictus</i>	Curculionidae	(Floate et al., 2011)
Coffee berry borer	<i>Hypothenemus hampei</i>	Scolytidae	(Vega et al., 2002)
Alfalfa weevil	<i>Hypera postica</i>	Curculionidae	(Klostermeyer, 1978; Hsiao & Hsiao, 1984)
Western corn rootworm	<i>Diabrotica virgifera virgifera</i>	Chrysomelidae	(Giordano et al., 1997; Barr et al., 2010)
Mexican corn rootworm	<i>Diabrotica virgiferae</i>	Chrysomelidae	(Giordano et al., 1997)
Northern corn rootworm	<i>Diabrotica barberi</i>	Chrysomelidae	(Roehrdanz & Levine, 2007)
Rice weevil	<i>Sitophilus oryzae</i>	Curculionidae	(Giordano et al., 1997)
Korean endemic firefly	<i>Luciola unmunsana</i>	Lampyridae	(Jeong et al., 2009)
Rice water weevil	<i>Lissorhoptrus oryzophilus</i>	Curculionidae	(Saito et al., 2005; Chen et al., 2012; Lu et al., 2013)
Flea beetle	<i>Aphthona nigricutis</i>	Chrysomelidae	(Roehrdanz et al., 2006)
Tobacco beetle	<i>Lasioderma serricorne</i> (Fabricius)	Anobiidae	(Kageyama et al., 2010)
Bread beetle or biscuit beetle	<i>Stegobium paniceum</i> (Linnaeus)	Anobiidae	(Kageyama et al., 2010)
Grain beetle	<i>Oryzaephilus surinamensis</i> (Linnaeus)	Silvanidae	(Kageyama et al., 2010)
Cowpea weevil	<i>Callosobruchus analis</i> (Fabricius)	Bruchidae	(Kageyama et al., 2010)
Cabinet beetle	<i>Anthrenus verbasci</i> (Linnaeus)	Dermestidae	(Kageyama et al., 2010)
Confused flour beetle	<i>Tribolium confusum</i>	Tenebrionidae	(Ming et al., 2015)

Conclusions

Wolbachia belongs to a diverse group of endosymbiotic bacteria which can manipulate the reproductive development of numerous arthropods. Tremendous achievements have been made from last few decades to understand the biology and mechanism of *Wolbachia*, specifically in the field of genetics and molecular biology through a numbers of advanced *Wolbachia* research tools and technologies. Now a days *Wolbachia* has become a potential biocontrol agent due to its various infectious phenotypic behaviors including incompatibility of cytoplasm, killing of the male embryo and induction of parthenogenesis and feminization which can change the biology of the host. Theoretical and experimental analysis show that *Wolbachia* may greatly affect the population of host species and efficiently used as a biocontrol agent in pest management strategies. Main purpose of this review is to highlight the significances and current discoveries of *Wolbachia* in various arthropods that lead a possible positive role in the field of IPM programs but still needs lot of key questions to be addressed like” can *Wolbachia* broadly used as biocontrol agent? On what conditions it behave like parasitic or mutualistic? Exact phenomena of this intracellular bacterium to manipulate host reproductions? Great attention is likely to be made to answering of these questions and next few years of *Wolbachia* studies therefore promises to be an exciting one.

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Conflict of interest

Authors would hereby like to declare that there is no conflict of interests that could possibly arise.

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