



Costs and benefits of symbiosis between a bean beetle and *Wolbachia*



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Wolbachia are a major symbiont of arthropods and nematodes. They can manipulate host reproduction in order to spread in host populations, but *Wolbachia* manipulation often incurs costs to the host species itself and/or provides benefits to the host. Because the fitness effects of *Wolbachia* infections differ between host species, fitness components of the host have to be carefully investigated. However, it is still relatively understudied. Here, we investigated effects of *Wolbachia* infection on life history and reproductive traits in *Callosobruchus chinensis*. This is a host in which the prevalence of *Wolbachia* and the cytoplasmic incompatibility (CI) it causes have been well reported. However, excluding research related to CI, there is little information about the effects of *Wolbachia* infection on traits of *C. chinensis*. We found that *Wolbachia* infection had positive effects on the life history and reproductive traits of *C. chinensis* males and females, with the exception of a negative effect on female fecundity. Nevertheless, *Wolbachia*-infected females are thought to have the advantage of reproduction because of complete CI in eggs from an uninfected female mated with an infected male. These results suggest that *Wolbachia* infection affects the life history and sexual selection of *C. chinensis* populations.

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Symbiosis is widespread in nature, and symbionts play ecologically and biologically important roles in their hosts. Numerous studies have reported on symbiont–host relationships such as mutualism and parasitism in various taxa (Bush, 2001; Roossinck, 2011). Symbionts can provide benefits or costs to a host's fitness, leading to a variety of effects from fatality (Pannebakker, Loppin, Elemans, Humblot, & Vavre, 2007) to weakness or no effect on the host's survival and traits (Ezenwa, Gerardo, Inouya, Medina, & Xavier, 2012).

Bacteria of the genus *Wolbachia*, bacterial symbionts, prevail widely in arthropods and nematodes (reviewed in Weeks, Reynolds, & Hoffmann, 2002; Werren, 1997). They are found in reproductive tissues of host species and are transmitted vertically from mother to offspring. It has been reported that *Wolbachia* drastically manipulates reproduction in various host species. To spread into a host population, *Wolbachia* kill male hosts in their early developmental stages (male killing, Hurst & Jiggins, 2000; Hurst et al., 1999; Jiggins, Hurst, & Majerus, 1998), or transform

them from genotypic male to phenotypic female (feminization, Bouchon, Rigaud, & Juchault, 1998; Hiroki, Kato, Kamito, & Miura, 2002; Kageyama, Nishimura, Hoshizaki, & Ishikawa, 2002; Negri, Pellecchia, Mazzoglio, Patetta, & Alma, 2006; Rousset, Bouchon, Pintureau, Juchault, & Solignac, 1992) because *Wolbachia* are inherited from mothers only. In haplodiploid species, *Wolbachia* induce thelytoky parthenogenesis (Stouthamer, Breeuwer, Luck, & Werren, 1993; Weeks & Breeuwer, 2001).

Of all *Wolbachia* manipulations, cytoplasmic incompatibility (CI) is the most common and has been reported in various host species (Dobson, 2004; Turelli & Hoffmann, 1995). CI results in the death of eggs from uninfected females mated with infected males in their early developmental stages (Dobson, 2004; Turelli & Hoffmann, 1995). CI-inducing *Wolbachia* are likely to confer a reproductive advantage on infected females compared with uninfected females because they are compatible with both infected and uninfected males. *Wolbachia* infection can confer a benefit on hosts through protection from viruses (Hedges, Brownlie, O'Neill, & Johnson, 2008; reviewed in Martinez et al., 2014). Furthermore, increased reproductive success of infected individuals has been reported in several species (Dong, Wang, Hu, & Jia, 2007; Fry & Rand, 2002; Fry, Palmer, & Rand, 2004; Girin & Boulétreau, 1995; Vavre, Girin, & Boulétreau, 1999; Wade & Chang, 1995). For example, *Wolbachia*

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are associated with increased host fecundity in *Trichogramma bourarachae* (Vavre et al., 1999). *Wolbachia* also improve hatching rates, female survival and fecundity in *Aedes albopictus* (Dobson, Rattanadechakul, & Marsland, 2004). This increased host fitness should spread *Wolbachia* in the host population. Similar findings have been reported in Rickettsia–host studies (Hendry, Hunter, & Baltrus, 2014; Himler et al., 2011).

In contrast, CI-inducing *Wolbachia* infection reduces male fitness because their sperm is incompatible with eggs of uninfected females. Fitness loss due to *Wolbachia* infection also occurs in females infected with male-killing *Wolbachia* (Fialho & Stevens, 2000). Furthermore, *Wolbachia* infection itself is known to impose physiological and fitness costs on its hosts (Stouthamer, Breeuwer, & Hurst, 1999; Werren, Baldo, & Clark, 2008). Such direct costs of *Wolbachia* infection per se have been well investigated in *Drosophila simulans*; negative effects of infection have been detected in many fitness-related traits such as fecundity (Hoffmann, Turelli, & Harshman, 1990), adult longevity (Fleury, Vavre, Ris, Fouillet, & Bouletreau, 2000), male fertility and sperm production (Champion de Crespigny & Wedell, 2006; Snook, Cleland, Wolfner, & Karr, 2000) and immune defence (Fytro, Schofield, Kraaijeveld, & Hubbard, 2006). On the other hand, several studies suggest that *Wolbachia* have little or no effect on host reproductive traits other than the CI effect (e.g. Poinot & Merçot, 1997). As mentioned above, *Wolbachia* infections strongly affect host biology; however, fitness benefits and costs may depend on the host species, genotype and sex (Clancy & Hoffmann, 1997; Fry & Rand, 2002; Olsen, Reynolds, & Hoffmann, 2001; Turelli & Hoffmann, 1995), and thus host fitness components should be carefully investigated (Fleury et al., 2000).

Wolbachia are thought to affect both sexual selection and reproductive strategies in the host (Champion de Crespigny & Wedell, 2006) because they bias the sex ratio towards (infected) females (Charlat et al., 2007; Hatcher, 2000; Jiggins, Hurst, & Majerus, 2000; Moreau, Bertin, Caubet, & Rigaud, 2001). Also, costs of *Wolbachia* infection to both female and male fitness are predicted to promote the evolution of mechanisms that avoid the deleterious effects of *Wolbachia* (Champion de Crespigny, Butlin, & Wedell, 2005; Champion de Crespigny, Pitt, & Wedell, 2006; Champion de Crespigny & Wedell, 2006; Hatcher, 2000). Preference for compatible mates before and after copulation, which biases offspring paternity, may be a potential strategy for overcoming the deleterious consequences of *Wolbachia* infection (Champion de Crespigny et al., 2006; Hoffmann et al., 1990; Zeh & Zeh, 1996, 1997). Female preference for uninfected males evolves because uninfected females that prefer compatible males avoid the reproductive costs of CI (Vala, Egas, Breeuwer, & Sabelis, 2004). Likewise, uninfected males prefer uninfected females to avoid a decrease in fitness by male-killing *Wolbachia* (Jiggins et al., 2000). Thus, investigating how *Wolbachia* infection affects the fitness of male and female hosts could lead to a much deeper understanding of sexual selection, and the evolutionary and ecological consequences of *Wolbachia* dynamics. However, to date, the subjects of such studies seem to have been limited to a restricted subset of insect taxa, for example *Drosophila* flies and *Trichogramma* wasps (see Werren, 1997). Additional studies are required to assess host fitness consequences of *Wolbachia* infection.

The adzuki bean beetle, *Callosobruchus chinensis*, is a cosmopolitan insect, and nearly 100% simultaneous infection by three strains of *Wolbachia* has been reported in all Japanese populations that have been screened (Kondo, Ijichi, Shimada, & Fukatsu, 2002; Kondo, Nikoh, Ijichi, Shimada, & Fukatsu, 2002). One (wBruAus strain) of the three *Wolbachia* strains is in the host genome as a genome fragment (Kondo, Ijichi, et al., 2002; Kondo, Nikoh, et al., 2002), and the others (wBruCon and wBruOri) are in the host's

cells, and cause CI between *Wolbachia*-infected fathers and uninfected mothers (Kondo, Ijichi, et al., 2002). The mating system and life history of *C. chinensis* have been well studied (Katsuki & Lewis, 2015; Katsuki & Miyatake, 2009; Shinoda & Yoshida, 1990; Umeya, 1987). However, the results of these studies lack information about the effects of *Wolbachia* infection on the life history, reproduction and sexual selection of *C. chinensis*, and thus this is the focus of this study. Here, to investigate whether *Wolbachia* infection affects life history and mating strategies in *C. chinensis*, we first compared the life history traits larval survival, developmental period, adult longevity, body size and locomotion ability of *Wolbachia*-infected and uninfected individuals that had been cured by antibiotics. We then investigated the reproductive traits mating duration, fecundity and the number of sperm transferred into the female's spermatheca per mating of infected and uninfected individuals.

METHODS

Insects

In *C. chinensis*, females lay eggs on the surface of beans, and larval development and pupation are completed entirely in a single bean (Umeya, 1987). Adults that emerge from beans are sexually mature (Nakamura, 1971). In this study, we used the tsC98 strain for the isofemale line of *C. chinensis*, which originated from adults collected in Tsukuba, Japan, in 1998 (Kondo, Nikoh, et al., 2002; Kondo, Shimada, & Fukatsu, 1999). This strain has since been maintained on adzuki beans, *Vigna angularis*, as the larval medium and oviposition substrate at 25 °C, 60% relative humidity, and with a photoperiod cycle of 14:10 h (light:dark). The stock is formed with approximately 300 adults per generation and maintained in a petri dish (diameter 90 mm, depth 10 mm) containing an excess of adzuki beans. This population has been maintained over 10 years under laboratory conditions. To eliminate the density effect in the present experiments, females were allowed to lay one egg on the surface of beans and extra eggs were removed. Each bean with one egg was placed in a well of 48-well tissue culture plates (Cellstar; Greiner Bio-One, Frickenhausen, Germany) until adult emergence (see Harano and Miyatake (2005) for details). After emerging, adults were individually placed in a well of new plates. Thus, the adults did not interact with conspecifics until the experiments were performed.

Infected and Uninfected Populations

As noted in Kondo, Ijichi, et al. (2002) and Kondo, Nikoh, et al. (2002), individuals of this population of *C. chinensis* are infected simultaneously with three distinct *Wolbachia* strains designated wBruCon, wBruOri and wBruAus. The triple infection affects nearly 100% of this population, and is also prevalent in the field at an average rate of 94% (Kondo, Ijichi, et al., 2002). The three strains of *Wolbachia* cause different levels of CI: complete and partial incompatibility are caused by wBruCon and wBruOri, respectively, but not by wBruAus (Kondo, Ijichi, et al., 2002). Interestingly, the wBruAus strain has no microbial entity, but is a genome fragment of the *Wolbachia* endosymbiont transferred to the X chromosome of the host insect. Thus, we removed wBruCon and wBruOri from the *C. chinensis* population using antibiotics: both strains can be easily eliminated with this treatment, which is not the case for wBruAus (Kondo, Ijichi, et al., 2002). This is a standard method for eliminating *Wolbachia* (e.g. Champion de Crespigny et al., 2006; McMeniman et al., 2009; Snook et al., 2000). Briefly, the *Wolbachia*-infected adults were cured by adding tetracycline hydrochloride to water at a concentration of 0.05% for two generations. Success was confirmed at the third generation using PCR: *Wolbachia* infection status can be determined using PCR for the universal

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