



## *Wolbachia* induces costs to life-history and reproductive traits in the moth, *Ephestia kuehniella*



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### ABSTRACT

The intracellular endosymbiont *Wolbachia pipientis* is well-known as one of the most common bacterial symbionts of arthropods. Recently, research has focused on the potential to utilize *Wolbachia* as a biocontrol agent of agricultural and medical pest insect species. *Wolbachia* blocks host infection from other pathogens and viruses in some species, however, it can also influence host life-history and reproductive traits. Therefore, in order to understand the biological impact and potential economic utility of *Wolbachia*, it is necessary to investigate the effects of *Wolbachia* infection on host traits. We compared life-history and reproductive traits between *Wolbachia*-infected and cured population in Mediterranean Flour Moth, *Ephestia kuehniella*. *E. kuehniella* is well known as a pest of stored products, and when infected with *Wolbachia*, it exhibits cytoplasmic incompatibility between uninfected females and infected males. We found that *E. kuehniella* suffers costs as a result of *Wolbachia* infection, through decreased larval survival and adult longevity, and prolonged developmental period. Moreover, reproductive performance was greater in the uninfected population, when excluding the effect of cytoplasmic incompatibility. Our results indicate that *E. kuehniella* suffers deleterious effects on both life-history and reproductive traits as a result of being infected with *Wolbachia*. We suggest such costs should be considered when evaluating the efficacy of utilizing *Wolbachia* in pest control.

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### 1. Introduction

The intracellular endosymbiont *Wolbachia pipientis*, of the *Rickettsia* sp. of bacteria, is well-known as one of the most common bacterial symbionts of arthropods, estimated to infect 40–50% of terrestrial species (Weinart et al., 2015; Zug and Hammerstein, 2012). *Wolbachia* are of particular interest to behavioral ecologists studying arthropods, due to its ability to manipulate the reproduction of its hosts. The endosymbiont is transmitted to all progeny, sons and daughters, from the infected mother via the cytoplasm of the egg; therefore, male sperms are essentially a dead-end for the bacterium (reviewed in O'Neill et al., 1997). As a result, *Wolbachia* have evolved a number of innovative mechanisms by which it increases its transmission (reviewed in Werren et al., 2008). In some amphipods, the bacteria feminizes genetic males.

Phenotypically, and reproductively, the males resemble and act like females, thereby effectively increasing the proportion of females in a given population, which in turn increases the spread of the *Wolbachia*. Similarly, in some species of arrhenotokys wasp, *Wolbachia* induce parthenogenesis, again thereby increasing the proportion of females, and in turn maximizing its transmission. In some insects such as the butterfly *Hypolimnas bolina*, *Wolbachia* act as a 'male-killer,' killing males in a given brood early in development; again, this results in an increase of the proportion of females.

The most common mechanism by which *Wolbachia* increase its transmission is via cytoplasmic incompatibility (CI). When uninfected females mate with infected males, up to 95% of the resulting brood are rendered inviable, and die (O'Neill et al., 1997). Combinations of infected females versus infected or uninfected males are compatible, as a result of an unknown 'rescue factor' produced in infected females' eggs which permit crossing with infected male sperm (Bourtzis et al., 1998; Riparbelli et al., 2007; Zabalou et al., 2008, but see Clark et al., 2008). As a result of CI, uninfected females have lowered reproductive success compared to infected females, who can mate with both infected and uninfected males.

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Thus, again, the bacterium promotes its transmission through the host population (Hoffmann et al., 1990).

Interest in *Wolbachia* has increased rapidly since the 1990s, as increasingly widespread and cheap molecular technologies have allowed researchers to easily identify infected individuals. However, the focus of the field has switched over time, from merely estimating prevalence of *Wolbachia* in wild and laboratory populations, to its importance as an evolutionary force (Duron and Hurst, 2013), to its utilization as a biocontrol agent of agricultural and medical pest insect species (reviewed in LePage and Bordenstein, 2013). For example, it has been shown that *Wolbachia* blocks Zika virus isolates in the mosquito *Aedes aegypti* in Brazil, the location of the recent Zika epidemic (Dutra et al., 2016). *Wolbachia*-induced resistance against dengue virus has been also found in *A. aegypti* (Walker et al., 2011; Bian et al., 2010). *Wolbachia* infection is known to activate the host immune system against other virus and pathogens (Xi et al., 2008; Kambris et al., 2009). Further, Zhang et al. (2016) have shown promise in utilizing a combination of the Sterile Insect and Incompatible Insect Techniques in *Aedes albopictus* mosquitoes infected with three strains of *Wolbachia*, under semi-field conditions, in order to suppress host population productivity.

Yet, other than in model species such as *Drosophila melanogaster* (Champion de Crespigny et al., 2006), or species of high medical or economic interest such as *Aedes* sp. (e.g. Dutra et al., 2016; Zhang et al., 2016) and the Mediterranean fruit fly crop pest (e.g. Sarakatsanou et al., 2011), the basic behavioral and physiological biology of the *Wolbachia*-host interaction is still unknown for the majority of the hosts which *Wolbachia* is known to infect. It has been shown that, despite the costs of CI to uninfected females within a population, there can be benefits of harboring *Wolbachia*. For example, in some species *Wolbachia* is an obligate endosymbiont of the host. In the bedbug *Cimex lectularius*, the bacterium is essential for the growth and reproduction of the host, as a result of the provision of crucial B vitamins (Nikoh et al., 2014). Similarly, in the parasitic wasp *Asobara tabida*, *Wolbachia* is required for oogenesis (Dedeine et al., 2001). A number of studies have also shown that *Wolbachia* can confer an advantage to the host by affording protection against pathogens such as other bacterial symbionts, fungi, and viruses (reviewed in Zug and Hammerstein, 2015). In contrast, in some species, above and beyond the costs associated with CI, hosts can suffer additional costs to, for example, male reproductive competitiveness (e.g. Champion de Crespigny and Wedell, 2006), female fecundity (e.g. Perrot-Minnot et al., 2002), and adult longevity (e.g. Carrington et al., 2010). The effects of *Wolbachia* on the host have also been examined in some more diverse taxa (e.g. in the spider mite; Vala et al., 2004, a *Drosophila* parasitoid; Fleury et al., 2000, *Tribolium confusum*; Wade and Chang, 1995, and a bean beetle; Okayama et al., 2016). However, to understand the biological impact and potential economic utility of *Wolbachia* in pest control, it is necessary to investigate the effects of infection on host life-history and reproductive traits in a greater variety of taxa.

The Mediterranean Flour Moth, *Ephestia kuehniella*, is a cosmopolitan pest of stored products such as flour; the larvae infest the products and cause considerable economic damage. The adults are polyandrous and females produce over 100 eggs over the course of their lifespan. The sterile insect technique via radiation has been considered as a method of controlling *E. kuehniella* (Ayvaz et al., 2007), however the use of *Wolbachia* has not been. Potentially crossing males with strong CI-inducing *Wolbachia* could decrease uninfected female fitness, resulting in suppression of the population. It has been reported that *E. kuehniella* populations in Japan are infected by *Wolbachia* (Ikeda et al., 2003; Kageyama et al., 2010; Sasaki and Ishikawa, 1999) and that they suffer CI as a result of

*Wolbachia* infection. For example populations from Yokohama and Tsuchiura population exhibited CI of 83.1% and 39.2% respectively (Sasaki and Ishikawa, 1999). Additionally, *Wolbachia* infected males exhibit a reduction in the numbers of sperm they transfer to females (Lewis et al., 2011a). However, nothing is known with regards the effects of *Wolbachia* on other life-history and/or reproductive traits in this species. Here, we examine the effect of *Wolbachia* on reproductive and life-history traits in *E. kuehniella*. By comparing *Wolbachia*-infected and uninfected populations, we assess the impact of *Wolbachia* on development time, adult body size, adult longevity, male mating performance, and female reproductive success.

## 2. Materials and methods

### 2.1. Stock culture

The stock population of *E. kuehniella* used in this study originated from adults collected in Yokohama, Japan, approximately 20 years ago, and is naturally infected with a single strain of group A *Wolbachia* inducing ~80% CI (Sasaki and Ishikawa, 1999; Lewis et al., 2011a). This population has since been maintained on a larval medium consisting of wheat bran, dried yeast and glycerol (20:1:2 w/w) at 25 °C, 60% relative humidity, and with a photoperiod cycle of 16L:8D (see Sasaki and Ishikawa, 1999 for details). As the moths have a generation time of two months, we assumed that they had been maintained under these laboratory conditions for approximately 120 generations at the time of our experiment, which was conducted in 2011. The population has been maintained with several hundred adults per generation since it was established, thereby minimizing the possible effects of inbreeding.

### 2.2. Generation of the uninfected population

Due to partial CI expression in *E. kuehniella* (Sasaki and Ishikawa, 1999), the population utilized includes both *Wolbachia* infected and uninfected individuals. We therefore generated an uninfected population via curing with antibiotics; the comparison of infected and uninfected individuals is a standard method of examining the effects of *Wolbachia* on the host (e.g. Snook et al., 2000; Champion de Crespigny and Wedell, 2006). Briefly, an infected population was established by selecting only *Wolbachia*-infected males and females (see Lewis et al., 2011a), then a sub-set of the *Wolbachia*-infected population was cured by adding tetracycline hydrochloride to the larval medium at a final concentration of 0.04%, for two generations (Sasaki and Ishikawa, 1999). The “cured” uninfected population was maintained for two generations prior to the experiment, under the same conditions as the infected population, in order to allow it to recover from potential detrimental effects of antibiotic-supplementation to insect rearing media (Graf and Benz, 1970). Infection status of the uninfected and infected populations was subsequently confirmed by PCR for the universal *Wolbachia*-specific primers wsp81F and wsp691R (Zhou et al., 1998).

### 2.3. Development time, adult longevity, and body size

All rearing experiments were conducted in a chamber maintained at the same rearing conditions described above. Females and males from the infected and uninfected populations were allowed to mate freely and lay eggs for twenty-four hours. Fifty eggs were then removed from each, and reared with an excess of the larval medium (100 g) to investigate development time and survival from egg to adult. Sexual discrimination of larvae in the early developmental stages is impossible, therefore we pooled survivors from egg to pupa of both sexes. Development time was assessed daily.

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