Effects of host plants, temperature regimes, and mating scenarios on the population dynamics of the cabbage whitefly *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae)

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Für meine Familie

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Summary

Within the last decade, the cabbage whitefly has become a major agricultural pest for *Brassica* crops, which has influenced the agricultural productivity of cabbage (*Brassica oleracea convar. capitata* L.) Brussels sprouts (*Brassica oleracea var. gemmifera* DC.), cauliflower (*Brassica oleracea var. botrytis* L.), kale (*Brassica oleracea var. sabellica* L.), kohlrabi (*Brassica oleracea var. gongylodes* L.), savoy cabbage (*Brassica oleracea convar. capitata var. sabauda* L.), and broccoli (*Brassica oleracea var. italica Plenck*). The current population increase of this species could be explained by climate change with warmer winters, increasing cultivated areas of oilseed rape and *Brassica* cover crops, and the development of insecticide resistant strains of cabbage whitefly. In the past, the cabbage whitefly was known as a non-significant pest of *Brassica* crops, which is partly why its biology has only been marginally studied. In this respect, exploring the biological parameters of *A. proletella* is likely to be of great value to understand the population dynamics of this insect species as well as to discover the reasons behind its current outbreak.

The biological parameters of *A. proletella* on different host plants were examined in a greenhouse experiment to assess their suitability for the cabbage whitefly. The impact of constant and alternating temperature regimes on the major life cycle component of cabbage whitefly were investigated in growth chamber-experiments. The influence of mating history on the population dynamics of this species was also examined and evaluated under different conditions.

1. Various biological traits (fecundity, pre-oviposition period, survival rate, sex ratio) of *A. proletella* were studied on winter oilseed rape, kale, cabbage, and kohlrabi to assess the suitability of these host plants.
   a. *A. proletella* was more fecund on winter oilseed rape than kale, kohlrabi, and cabbage.
   b. Host plants influenced the pre-oviposition period of *A. proletella*, resulting in shorter pre-oviposition periods on oilseed rape.
   c. Survival rate of *A. proletella* adults was strongly influenced by host plants, which was the lowest on white cabbage.

d. The sex ratio of *A. proletella* offspring was significantly influenced by the host plant, with the highest female ratio being on kale and winter oilseed rape.
e. Winter oilseed rape was therefore determined to be the most suitable host plant among all those considered.

2. Evaluating the influence of fluctuating temperatures versus their equivalent constant average on reproduction parameters (fecundity, mean daily fecundity, age-specific fecundity, survival rate, sex ratio) of cabbage whitefly.
   a. The 23 °C fluctuating temperature regime decreased the survival rate of cabbage whitefly males in comparison to their equivalent constant temperature mean.
   b. The 20 °C fluctuating temperature increased the total fecundity of cabbage whitefly females in comparison to their representative constant temperature mean.
   c. The pattern of the age-specific fecundity curve under fluctuating temperature regimes differs from those at constant regimes, leading to a higher peak throughout the earlier stages of the lifespan and a sharper decrease as females become older.
   d. The temperature regime did not affect the sex ratio of cabbage whitefly.
3. The influence of mating scenarios (life span mated female and male; virgin female and male; short time mated females) on longevity, survival rate, total fecundity, and sex ratio of *A. proletella* was examined under constant temperature regimes of 20°C. In addition, the first two experiments also evaluated the influence of mating scenarios on the survival rate and oviposition of cabbage whitefly.
   a. The total number of eggs of eight day mated females was slightly lower than those of virgin and life span mated females.
   b. The mating history did not influence the life span or survival rate of *A. proletella* females or males.
   c. The sex ratio of life span mated females was lower than that of short time (eight day) mated females, whereas virgin females produced purely male offspring.
   d. In the greenhouse experiment the mating history did not affect the survival rate and oviposition of the cabbage whitefly.

e. Under fluctuating temperature conditions, the influence of mating scenario was only detectable under the 20 °C fluctuating temperature regime, where the fecundity of eight day mated females was reduced in comparison to the virgin and life span mated females.

General introduction

Vegetable *Brassica* crops are some of the most important cultivated vegetables crops in Germany with cultivation covering 18,802.1 ha. This includes cauliflower (*Brassica oleracea var. botrytis* L.) which occupies 3 268.6 ha, broccoli (*Brassica oleracea var. italica* Plenck) 2 194.6 ha, Chinese cabbage (*Brassica rapa supbs. pekinensis* Lour. hanelt) 850.6 ha; kale (*Brassica oleracea var. sabellica* L.) 959.3 ha, kohlrabi (*Brassica oleracea var. gongylodes* L.) 1 830.8ha; Brussels sprouts (*Brassica oleracea var. gemmifera* DC.) 474.3 ha, red cabbage (*Brassica oleracea convar. capitata var. rubra* L.) with 2 109.1 ha, white cabbage (*Brassica oleracea convar. capitata var. alba*) 6 166.0 ha, and savoy cabbage (*Brassica oleracea convar. capitata var. sabauda* L.), which is planted over 948.5 ha of land (Statistisches Bundesamt, 2017). However, the production of these crops can be threatened by several herbivorous insects such as cabbage whitefly (*Aleyrodes proletella* L.), green peach aphid (*Myzus persicae* Sulzer); cabbage aphid (*Brevicoryne brassicae* L.), thrips (*Thrips tabaci* Lindeman), cabbage flea beetles (*Phyllotreta* spp.), cabbage gall weevil (*Ceutorhynchus pleurostigma* Marsh.), small cabbage white (*Pieris rapae* L.), cabbage root fly (*Delia radicum* L.), the cabbage moth (*Mamestra brassicae* L.), and the diamondback moth (*plutella xylostella* L.) (Crüger and Backhaus, 2002).

Surprisingly, the cabbage whitefly has been gaining more importance as a key pest of *Brassica* crops (Richter and Hirthe, 2014; Muñiz and Nebreda, 2003; Ramsey and Ellis, 1996) and it is today one of top three most important insect pests that attack cabbage cultivars (R. Meyhöfer, personal communications). The reasons for this increasing problem are not well understood, but the increase in their population could be linked to the impacts of climate change. For instance, warmer, shorter winters could increase the survival rate of overwintering adults. As a result, the density of the starting population that invades the *Brassica* crops in the early season will rise as well. In addition to milder winters, an increase in summer temperatures could also influence the cabbage whitefly population. It has been reported that increasing summer temperatures can accelerate the life cycle time, enhance the oviposition, and increase the population growth of an insect (Bale et al., 2002; Curnutte et al., 2014; Porter et al., 1991). Furthermore, temperature could also indirectly influence the population

growth of herbivorous insects through changing plant quality. Pereira et al. (2002) reported that temperature might change secondary metabolites such as glucosinolate concentrations in the plant, which in turn could affect the population growth of cabbage whitefly. Another factor that could influence population growth is the increasing cultivation area of oilseed rape, which offers suitable overwintering host plants for the cabbage whitefly (Richter and Hirthe, 2014). In addition, cabbage whitefly can benefit from the increasing cultivation areas of *Brassica* cover crops (White mustard *Sinapis alba* L. and oilseed radish *Raphanus sativus* L. *ssp.* Oleiferus), which provide this species with host plants to hibernate and reproduce. From another point of view, oilseed rape production is associated with intensive insecticide use such as Neonicotinoide and Pyrethroide (Jeschke et al., 2011; Slater et al., 2011; Williams, 2010) , which can indirectly decrease the vulnerability of cabbage whitefly, as a non-target species, to such insecticides or lead to the development of resistant cabbage whitefly strains (B. Ulber, personal communications).

Cabbage whitefly is a polyphagous phloem sucker that invades a wide range of host plants. According to Mound and Halsey (1978) this species was found on a broad range of host families, e.g. Balsaminaceae, Berberidaceae, Campanulaceae, Compositae, Brassicaceae, Euphorbiaceae, Fagacea, Leguminosae, Papaveraceae, Ranunculaceae, Scrophulariaceae, and Umbelliferae, but preferring to obtain its nutrition from cruciferous vegetables. This whitefly species is native to continental Europe, but it has been recorded in many parts of the world, including Palearctic, Neotropical, and Pacific regions (Chen et al., 2007; Evans, 2007; Martin et al., 2000).

A. proletell is a small herbivorous insect, approximately 1.5 mm long, and has a piercing mouth parts for sucking (Hill and Hill, 1994). Their wings are marked with four gray spots, which distinguish it from other whitefly species. The body, as well as the wings, is covered with white wax, which gives the cabbage whitefly their powdery white appearance (Byrne, 1991). Males are smaller than females and develop from unfertilized eggs, whereas females develop from fertilized eggs (Byrne, 1991; Byrne and Devonshire, 1996). Adult females lay their eggs in circular or semicircular clutches, usually in groups of 30 to 40 eggs, surrounded with a thin white wax (Broekgaarden et al., 2012; Martin et al., 2000). Within an incubation period of 10 to 20 days, depending

on the surrounding environmental conditions, the eggs develop into scale-like nymphs (Nebreda et al., 2005). As the first nymphal stage has functional legs, they crawl searching for a suitable place to feed and settle. The following nymphs (second, third and fourth instar nymphs) lose their functional legs and develop by shedding their larval skin. Nevertheless, the fully grown fourth instar pupates without molting within the nymphal skin (Byrne, 1991). Shortly before hatching, the red eyes of adults can be seen through the pupae skin. The entire life cycle takes approximately three to four weeks, depending on the host plant and temperature (Alonso et al., 2009; Barro and Hart, 2000; Nebreda et al., 2005). In addition, El-Helaly et al. (1977) reported that the development time of eggs, nymphs and pupae could be affected by the length of the photophase. The development of nymphs under short photoperiod conditions could induce female diapause (Adams, 1985). Cabbage whitefly hibernate as adults on oilseed rape, cover crops, weeds (e.g. *Chelidonium majus* L.) or overwintering cabbage crops (e.g. winter cabbage and winter kale). Therefore, adults can be seen on the host plant throughout the year. Being a multivoltine insect species, the cabbage whitefly generates up to five overlapping generations per year (Chen et al., 2007; Crüger and Backhaus, 2002).

Both adults and juveniles feed by injecting their piercing mouthparts into the phloem vessels and extracting the plant sap. As a result of the feeding process, large amounts of sugary liquid, called honeydew is secreted. The covering of leaves with honeydew encourages black fungal growth (Bährmann and Moritz, 2002; Crüger and Backhaus, 2002; Hill and Hill, 1994). Coating the leaves with honeydew and black fungi decreases the growth rates of the plants. The contamination of plants with eggs, wax, larvae, and black fungi decreases the plant quality and marketability (Mound and Halsey, 1978; Schultz et al., 2010).

The control of this species is demanding and hard to accomplish as adults and nymphs are generally found on the underside of the leaves. This makes insect pest control a very difficult process, which has led to the majority of control to be based on chemical insecticides (Springate and Colvin, 2012; Trdan et al., 2003; Wyss and daniel, 2002). According to Springate and Colvin (2012) frequent applications of insecticides lead to resistant cabbage whitefly strains. A number of predators (*Coccinella undecimpunctata*

L., *Clitostethus arcuatus* Rossi) and parasitoids (*Encarsia tricolor* Förster, *Encarsia inaron* Walker) have been found to attack cabbage whitefly (Cabral et al., 2006; Huang et al., 2009; Loomans et al., 2002; Manzari et al., 2002; Mound and Halsey, 1978). However, neither biological nor chemical control have been able to dominate the control of this species (Loomans et al., 2002; Richter and Hirthe, 2014; Trdan et al., 2003); a high level of skill and timing is required.

Historically, cabbage whitefly has had negligible impact on the production of field *Brassica* crops (Iheagwan, 1977; Martin et al., 2000). Therefore, little attention has been given to this species leading to gaps in information about it. This lack of information includes the influence of temperature, host plant, and adult mating status on the *A. proletella* reproduction parameters and population dynamics. In contrast, the population dynamics and the reproduction parameters of the most important whitefly spices, *Bemisia tabaci* Gennadius and *Trialeurodes vaporariorum* Westwood, have been widely studied and reported (Campos et al., 2003; Coudriet et al., 1985; Gerling et al., 1986; Lorenzo et al., 2016; Manzano and van Lenteren, 2009; Nava-Camberos et al., 2001; Xie et al., 2011). These studies indicate that temperature is one of the most important factors that influence the specific life history traits of whiteflies. Although there is significant evidence indicating that the performance of ectothermic insects under fluctuating temperature regimes did not reflect those under the equivalent constant average (Lamb, 1961; Mironidis and Savopoulou-Soultani, 2008), to date, whiteflies studies have been performed under constant temperature regimes. Messenger (1964) reported that fluctuating temperature enhances the development time, longevity, and oviposition of the Spotted Alfalfa Aphid, *Therioaphis maculata* (Buckton), in comparison to the representative constant mean. Beck (1983) summarized the thermoperiodism of insects and indicated that the alternating temperature regime could not reflect their correspondent constant mean.

Host plant and host plant suitability are other important factors which also influence the biology of whiteflies. Several studies on the relationship between host plant and *B. tabaci* have reported that the oviposition, longevity, and sex ratio of whiteflies could be influenced by the host plant (Lin and Ren, 2005; Omondi et al., 2005; Qiu et al., 2011). On the other hand, it is widely reported that the mating history is an important

factor that influences the performance of an insect species (Ridley, 1988; Walker, 1980). For example, Horowitz and Gerling (1992) reported that the longevity of multiple mated female of *B. tabaci* was shorter than those of females that mated shortly after emergence. Furthermore, (Arnqvist and Nilsson, 2000) summarized the influence of mating in different insect taxa and reported that mating history could influence the biological traits of an insect species. In this respect, all essential factors that affect the population growth of whitefly should be taken into consideration when management strategies are developed.

Objective

As far as we know, knowledge about the population dynamics of *A. proletella* is rather scattered, and data on the reproduction parameters of this species is limited. This study, therefore, is aimed to fill the information-gaps on the biological parameters of this species by, a) understanding the influence of fluctuating temperatures and their equivalent constant average on *A. proletella* reproduction parameters, b) evaluating the relationship between the population dynamics of this species and their host plants, and c) investigating the impact of mating scenarios on the major life cycle component of *A. proletella*. A more comprehensive understanding of the links between these crucial factors and the basic biological parameters of *A. proletella* will contribute towards the improvement of forecasting models of *A. proletella* population growth, and subsequently leading to the development of management strategies to control this insect pest.

a. Evaluation of the reproduction parameters of *A. proletella* and its interactions with different host plants (Chapter 1)
    1. What is the influence of the host plant on the oviposition, pre-oviposition time, survival rate of adults, and sex ratio of cabbage whitefly?
    2. Is winter oilseed rape a suitable host plant for *A. proletella*?
b. The relationship between ambient temperature regimes and the biological parameters of *A. proletella* (Chapter 2)
    1. What influence does the ambient temperature have on the survival rate of adults, oviposition, and sex ratio of cabbage whitefly?
    2. What is the cabbage whitefly response to the fluctuating temperature regimes in comparison to the constant temperature regimes?
c. Understanding the biology and population dynamics of *A. proletella* (Chapter 1, 2 and 3)
    1. Exploring the basic biological parameters of *A. proletella* including the development time, mortality of developmental stages, fecundity, longevity, and sex ratio.
    2. Does the mating scenario influence the reproduction parameters of *A. proletella*?

Chapter 1

Life history parameters of *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae) on different host plants

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Chapter 2

Effects of constant and fluctuating temperatures on the biological traits of cabbage whitefly *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae)

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Abstract

Despite the fact that, *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae), has become a serious agricultural pest of *Brassica* crops, few studies so far have investigated the impact of temperature on the biological characteristics of this pest species. Laboratory studies were used to explore the influence of fluctuating temperature regimes (18 to 22 °C and 21 to 25 °C) and their equivalent constant means of 20 °C and 23 °C on the reproduction parameters of the cabbage whitefly. In addition, within each temperature regime the effect of mating scenario (64-day mated female and male; virgin female and male; eight day mated female) on the survival rate and oviposition of *A. proletella* adults was also evaluated. The survival rate of males as well as females was not affected by mating scenario. The oviposition of *A. proletella* females was also not influenced by the mating scenario, except under the 20 °C fluctuating regime where the oviposition of eight day mated females was significantly lower than that of the virgin and 64 day mated females. The survival rate of *A. proletella* adults was significantly affected by the temperature regimes. Overall, the oviposition of *A. proletella* was significantly affected by temperature regimes. The maximum total number of eggs was obtained under the 20 °C fluctuating temperature regime. The shapes of age-specific fecundity curves obtained under fluctuating regimes differ from those under constant regimes. At all temperature regimes, *A. proletella* females produced significantly more females than males. The sex ratio of *A. proletella* was not significantly affected by temperature regimes. These results demonstrate that the

alternating temperature regimes are not likely to represent the corresponding constant means. In this respect, all future population growth prediction models should take such differences into account.

Keywords: *Aleyrodes proletella,* cabbage whitefly, temperature regimes, fluctuating temperature, biological parameters.

Introduction

The Cabbage Whitefly, *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae), is a polyphagous insect that feeds on a wide variety of host plants within more than ten different host families (Martin et al., 2000; Mound and Halsey, 1978). It is native to Europe, but has spread worldwide (Dale et al., 1976; Evans, 2007).

Since the late 1990s, this insect has caused serious economic problems and was able to flourish in brassica cultivation areas across Europe, including Germany, Spain, and the U.K. (Muñiz and Nebreda, 2003; Ramsey and Ellis, 1996; Richter and Hirthe, 2014b). The reasons why *A. proletella* has become a major pest are not well understood and appear to be related to a combination of the following factors: a) increased cultivation of oil seed rape (*Brassica napus* L.), which can provide *A. proletella* with a suitable host plant to reproduce and overwinter (Richter and Hirthe, 2014b); b) climate change with temperate winters cause a decrease in overwintering mortality; and hot summers enhance the growth of insect populations and increase the generation number per year (Bale et al., 2002; Curnutte et al., 2014; Porter et al., 1991); and c) insecticide resistance (Springate and Colvin, 2012). Damage occurs either directly through sap sucking nymphs and adults, or indirectly by the excreted sugary sticky liquid known as honeydew, which enhances the growth of sooty mold (*Capnodium* sp.) (Hill and Hill, 1994). The presence of honeydew and sooty mold not only reduces the photosynthesis of the plant but it decreases produce quality (Martin et al., 2000; Schultz et al., 2010).

The entire life cycle of *A. proletella* takes three to four weeks, depending on environmental conditions and host plant (Alonso et al., 2009; Muñiz and Nebreda, 2003; Nebreda et al., 2005). The cabbage whitefly can produce up to four generations per year (Chen et al., 2007), which hibernate as adults on oil seed rape (*Brassica napus* L.) (Richter and Hirthe, 2014b), cover crops (white mustard (*Sinapis alba* L.), oilseed

radish (*Raphanus sativus* L. ssp. *oleiferus*), weeds like greater celandine (*Chelidonium majus* L.), or overwintering cabbage crops such as winter cabbage (*Brassica oleracea convar. capitata* L.), and winter kale (*Brassica oleracea var. sabellica* L.). The control of whitefly typically relies on chemical control such as Pyrethroid insecticide, which has lead to the development of resistant cabbage whitefly strains (Springate and Colvin, 2012). Biological control programs have been applied using the parasitoids *Encarsia tricolor* Förster (Schultz et al., 2010). In part due to the lack of information on cabbage whitefly biology neither the biological nor the chemical programs have been effective (Loomans et al., 2002; Richter and Hirthe, 2014a; Trdan et al., 2003).

Classified as a minor pest in the past (Iheagwan, 1977; Martin et al., 2000) little attention has been given to the biology of cabbage whitefly and its relation to environmental conditions such as temperature. In contrast, the influence of environmental factors on the fitness of the most important whitefly spices like *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood) has been broadly studied and reported (Gerling et al., 1986; Nava-Camberos et al., 2001; Xie et al., 2011). These studies indicate that temperature is a critical factor that influences the development time, lifespan, fecundity, and growth rate of those species. However, these studies were performed under constant temperature conditions. So far there are no studies investigating the influence of fluctuating temperatures versus their constant equivalent mean on the biology of whiteflies. Messenger (1964) and Lamb (1961) reported that constant temperature regimes do not reflect what occurs in nature. In addition, many studies reported that the influence of fluctuating temperature on the development time of an insect species could differ from their representative constant mean (Bahar et al., 2012; Beck, 1983). For instance, the development time of the diamondback moth, *Plutella xylostella* L., was accelerated under fluctuating temperatures in comparison with their specific constant means (Bahar et al., 2012). Messenger (1964) reported that the fluctuating temperatures positively affected the development time, lifespan, and oviposition of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton). Not just the fluctuating temperatures per se influence the life cycle of an insect, but also the amplitude of those fluctuating temperatures plays an important role (Auad et al., 2015; Mironidis and Savopoulou-Soultani, 2008).

The influence of temperature on major life cycle components of cabbage whitefly has not been extensively examined (Alonso et al., 2009). To the best of our knowledge, no such studies have been conducted for the cabbage whitefly and this is the first study that investigates the influence of fluctuating temperatures versus their representative constant means on the life history traits of *A. proletella*. This study therefore, aimed to investigate the effect of fluctuating temperature and the corresponding constant mean on cabbage whitefly reproduction parameters including: fecundity, survival rate, and sex ratio. A more comprehensive understanding of the influence of fluctuating temperature versus the corresponding constant mean on the population growth and population dynamics of *A. proletella* will contribute towards improved model prediction of *A. proletella* population growth and subsequently lead to management strategy refinements for this pest species.

Material and methods

Insects

The *A. proletella* females were collected from three regions in Germany (Braunschweig, Bonn, and Dresden). Fifteen whitefly colonies (five from each region) were developed by confining single females in rearing cages (60×60×60 cm), in order to obtain colonies that would host identical secondary endosymbiont species and minimize the genetic variability. The whitefly colonies were reared on Brussels sprout plants (*Brassica oleracea* var. gemmifera) in a growth chamber at 20 °C and a photoperiod of L16:D8. The determination of endosymbionts demonstrates that our 15 colonies contain identical secondary endosymbiont species (P.Hondelmann, IGPS - Dept. Phytomedicine, April 15, 2015). We selected one of the colonies established from Braunschweig and used this for the present experiment.

Plant material

Brussels sprouts (*Brassica oleracea* var. gemmifera cv.Maximus, Syngenta, Germany) were used as test plants, which were grown in a greenhouse in 14-cm plastic pots filled with potting compost (Klasmann-Deilmann Geeste, Germany) at 19-21 °C and 55-75 % RH. Plants were fertilized twice a week using 0.01 % flory-1 (N-P-K-Mg 0.18-6-12-2, Gebr. Riege oHG, Germany) and watered as necessary. At two months of age, Brussels sprout plants were moved to climate chambers and used for the experiment, fertilized and watered as described above.

Temperature regimes:

The following fluctuating temperature regimes 18-20-22-20 °C, 21-23-25-23 °C and their equivalent constant means of 20 °C and 23 °C were used. The fluctuating temperature regimes were held for 11 h at the maximum (i.e: 22 and 25 °C), 11 h at the minimum temperature (i.e: 18 and 21 °C) and for a recovery period of one hour at 20 and 23 °C, respectively [Figure. 1]. A photoperiod of L16:D8 was employed for all temperature regimes.

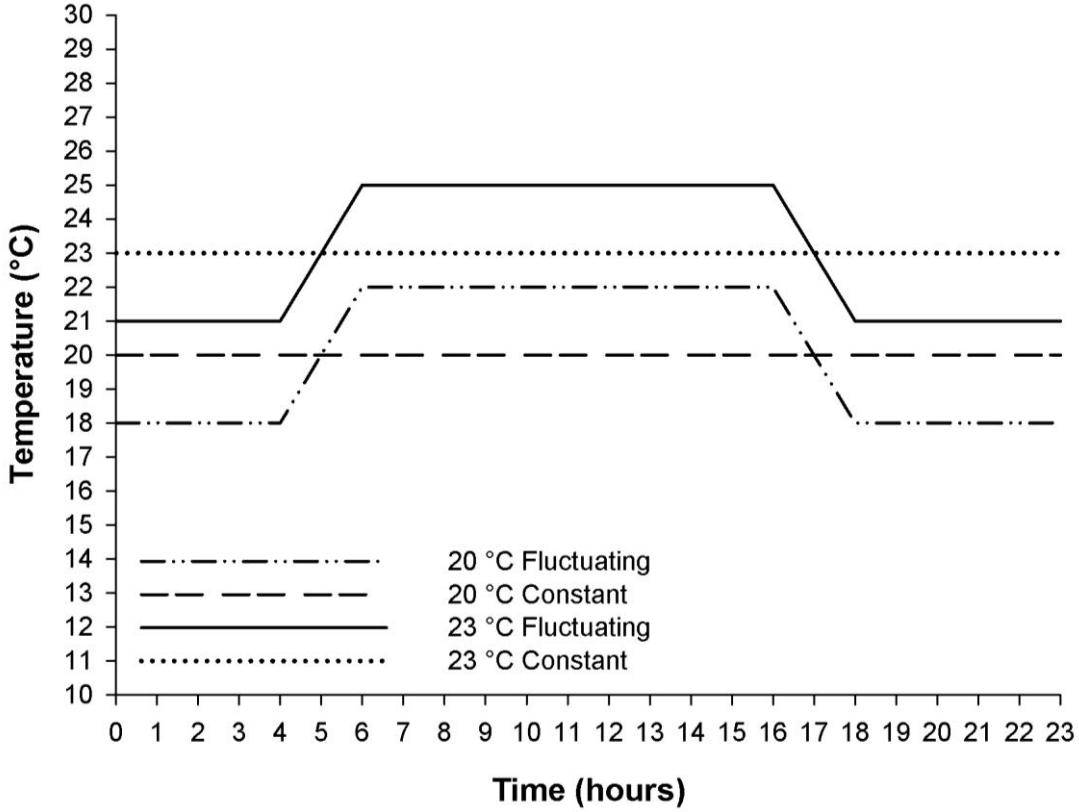

Figure 1: Schematic representation of fluctuating and constant temperature regimes.

Reproductive parameters

1. Acquirement of one-day old virgin adults

One day-old-virgin adults of *A. proletella* were obtained by applying the following procedure: Brussels sprout plants were maintained in a growth chamber at 25 °C with a photoperiod of L16:D8 and 55-75 % RH and were initially infested with *A. proletella* adults. Females were allowed to oviposit for 24 hours; thereafter, all adults were removed. Shortly before hatching, red eye pupae were moved to small Petri dishes (35×10mm) using a needle (one pupa per Petri dish). The Petri dishes contained pieces of Brussels sprout leaves placed on wet filter paper. Adults that hatched within 24 hours were considered equal in age. On emergence, the sex of one-day-old virgin adults was determined under a microscope (Zeiss, Stemi sv8, Germany).

2. Fecundity and survival rate measurements

To compare and evaluate the influence of temperature regimes on oviposition and the survival rate of *A. proletella*, clip cages were attached to the underside of the tenth

fully grown leaf (the numbering of leaves started with the youngest fully grown leaf). Thereafter, the following treatments were constructed within each temperature regime: a) 64-day mated females (64MF) and males (64MM): for this treatment, pairs of one-day-old virgin adults were placed individually in clip cages for the whole experimental period (64 days). b) Eight day mated females (8MF): where pairs of one-day-old virgin adults were individually placed in clip cages for eight days after which the males were removed. c) Virgin females (VF): one-day-old virgin females were individually confined in clip cages during the experimental period. d) Virgin males (VM): one-day-old virgin males were individually placed in clip cages during the experimental period. All differently treated adults were transferred to new leaves (the next younger leaf on the same experimental plant). This procedure was performed every four days until the end of the experiment, which was terminated after 64 days (due to the high mortality of adults under the 23 C° temperature regime). Eggs laid every four days were counted under a microscope (Zeiss, Stemi sv8, Germany). New clip cages were placed in the same position as the old cages to confine the eggs.

Additionally, the survival rate of adults was recorded daily throughout the experimental time. A random block design with eight replicates was used in each mating scenario as well as in each temperature regime.

3. Sex ratio

After adult cabbage whiteflies were removed and eggs counted, leaves bearing eggs were allowed to continue to grow for one week on mother plants. Then the leaves with clip cages were removed from the stem and the petioles transferred to glass tubes filled with water. The glass tubes were kept in the same chamber as the mother plants. After all *A. proletella* adults had hatched in the clip cages, adults were killed by placing the leaves in a freezer at -16 °C. The sex ratio of the adults was then determined using a microscope (Zeiss, Stemi sv8, Germany).

Statistical analysis

All statistical analyses were performed using the R statistical program version 3.2.3 (R Core Team, 2016).

To detect the influence of mating scenario on the survival rate of cabbage whitefly adults, the Kaplan-Meier survival analysis (log-rank test) was performed (Therneau and Grambsch, 2000). Due to the non-significant effect of the mating scenario on the survival rate of cabbage whitefly adults (see results), the survival rate data of males as well as of females was pooled across mating treatment for each temperature regime. To detect the influence of the temperature regimes on the survival rate of whitefly adults, a Kaplan-Meier survival analysis (log-rank test) was firstly performed. Thereafter, a non-constant hazard model using Weibull errors was used to reveal differences between temperature regimes (Crawley, 2013).

In order to analyze the influence of mating scenario on the total fecundity, generalized linear models (GLM) were fitted with quasi Poisson errors (R Core Team, 2016). The total number of eggs was then used as the dependent variable and mating scenario as the independent variable. The mean daily fecundity (total number of eggs laid during the experimental time divided by oviposition time) was analyzed using the linear model function (gls: linear model using generalized least squares) with the mean daily fecundity as the dependent and mating scenario as independent variable (R Core Team, 2016).

To analyze the influence of temperature regime on the mean daily fecundity and the total number of eggs, the fecundity data of virgin, 64-day, and 8-day mated females at 23 °C fluctuating, 23 °C constant, and 20 °C constant temperature regimes was pooled across mating scenarios due to the non-significant effect of mating treatment on fecundity (see results). Whereas, the fecundity data under the 20 °C fluctuating regime was pooled across virgin and 64-day mated females due to the insignificant differences between virgin and 64-day mated females under this temperature regime (see results). Thereafter, the above described analyses were repeated with the temperature regime as independent variable.

In order to analyze the influence of temperature regimes on the shape of the age-specific fecundity (eggs/ female/ four-days) curve, data was pooled across mating scenarios as described above and mixed-effect polynomial models for longitudinal data (lmer) (Bates et al., 2015) were fitted (by maximum likelihood). In this model we used temperature regimes and age of females (as cubic polynomial) as independent variables, whereas the number of eggs at four day intervals was used as the response variable. The random-effects structure of this model included whitefly (subject) as well as mating scenario (virgin, 64-day mated and eight-day old mated) as non-nested random effects. Because the number of replicates (whitefly) decreased towards the end of the experiment, this model was only fitted for the first 56 days of the experimental time.

To determine whether temperature regimes affect the sex ratio of whitefly offspring, males and females were grouped together as the response variable and analyzed using the general linear model with quasi binomial errors (Crawley, 2013). Additionally, binomial tests were performed to determine whether the sex ratio of cabbage white flies departed from the even sex ratio of 50:50 (Crawley, 2013).

Survival rate, total and daily fecundity graphics were developed using SigmaPlot (Systat Software, San Jose, CA). The age-specific fecundity plots were performed with the Package ‘effects’ in the statistical program R (Fox, 2003).

Results

Survival rate of *A. proletella* females and males

The mating scenario did not affect the survival rate of female *A. proletella* at 23 °C fluctuating (log-rank test: x^2 = 1.1, p = 0.58), 23 °C constant (log-rank test: x^2 = 0.3, p = 0.86), 20 °C constant (log-rank test: x^2 = 0.1, p = 0.93), and 20 °C fluctuating (log-rank test: x^2 = 3.4, p = 0.18) temperature regimes.

Similarly, the survival rate of virgin as well as 64-day mated males did not significantly differ within each tested temperature regime (23°C fluctuating: log-rank test: x^2 = 1.1, p = 0.87; 23 °C constant: log-rank test: x^2 = 0.3, p = 0.57; 20 °C fluctuating: log-rank test: x^2 = 1.5, p = 0.22; 20 °C constant: log-rank test: x^2 = 0.2, p = 0.62).

Moreover, the survival rate did not significantly differ between female (pooled data from virgin, 64-day, and 8-day mated females) and male (pooled data of virgin and 64-day mated males) whitefly adults within each temperature regime tested i.e. at 23 °C fluctuating (log-rank test: x^2 = 0.8, p = 0.35), 23 °C constant (log-rank test: x^2 = 0, p = 0.90), 20 °C constant (log-rank test: x^2= 1, p= 0.31), and 20 °C fluctuating (log-rank test: x^2 = 1.1, p = 0.30).

Temperature regimes significantly affected the survival rate of *A. proletella* females (pooled data of virgin, 64-day, and 8-day mated females) (log-rank test: x^2 = 13.6, p < 0.05), in that the survival rate of females was significantly lower at 23 °C fluctuating than those at 20 °C constant (z =-2.61, p < 0.05), and at 20 °C fluctuating temperature regimes (z = 2.77, p < 0.05). However, the survival rate of females at 20 °C fluctuating, 20 °C constant and 23 °C constant did not significantly differ from one another (23 °C fluctuating: 23 °C constant, *z* = 1.6, p = 0.28; 20 °C fluctuating: 20 °C constant, *z* = 0.58, p = 0.55; 23 °C constant: 20 °C constant, z = -1.57, p = 0.11; 20 °C fluctuating: 23°C constant *z* = -1.9, p = 0.05) [Figure. 2].

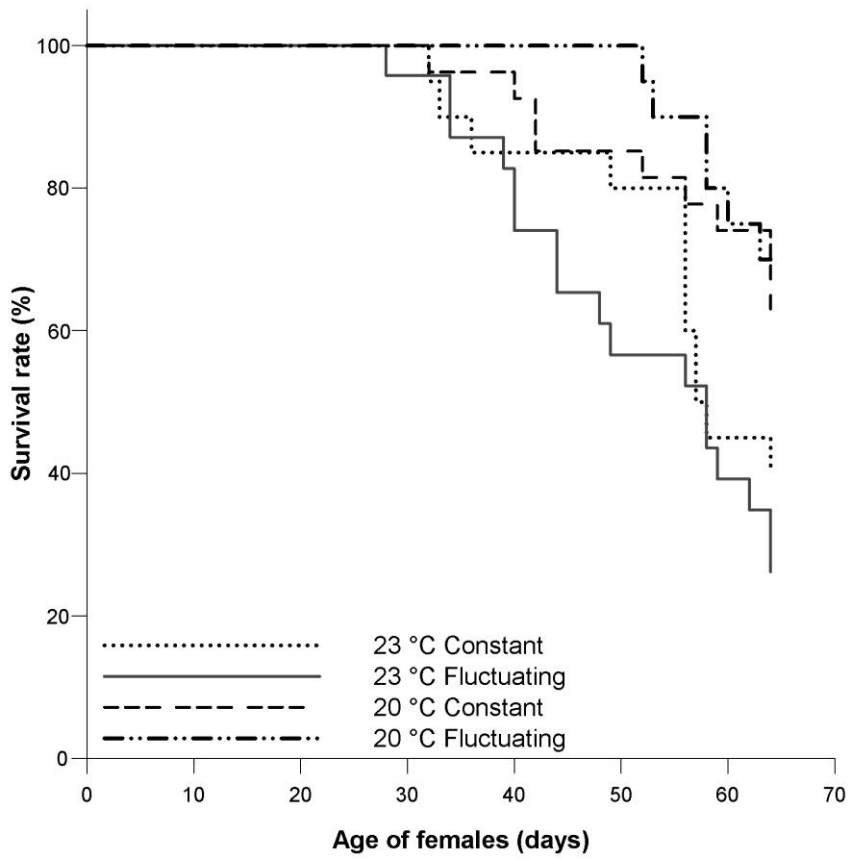

Figure 2: Survival rate of *A. proletella* females under different temperature regimes. log-rank test (P < 0.05).

The temperature regime significantly influenced the survival of *A. proletella* males (log-rank test: x^2 = 20.4, p < 0.001). The 23 °C fluctuating temperature significantly reduced the survival rate of males in comparison with the equivalent constant mean (z = 1.97, p < 0.05), whereas the survival rate at 20 °C fluctuating did not significantly differ from that of 20 °C constant temperature regime (z = -1.28, p = 0.19). Moreover, the survival rate of males at 23 °C fluctuating temperature significantly differed from that of 20 °C fluctuating (z = 3.01, p < 0.01) and the 20 °C constant temperature regime (z = -3.33, p < 0.001). In addition, the difference between 23 °C and 20 °C constant temperature regime was significant (z = -2.02, p < 0.05), while the difference between 23 °C constant and 20 °C fluctuating temperature regime was not significant (z = -1.04, p = 0.29) [Figure.3].

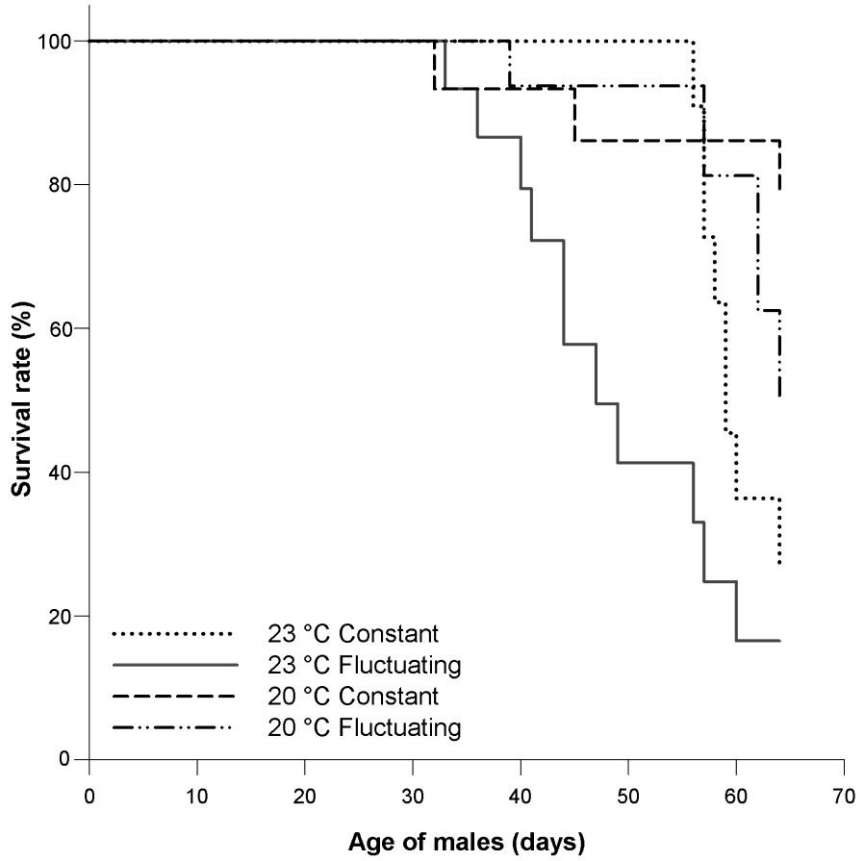

Figure 3: Survival rate of *A. proletella* males under different temperature regimes. log-rank test ($P < 0.05$).

Oviposition of *A. proletella*

Total number of eggs

For the 20 °C fluctuating temperature regime, the total number of eggs of eight day mated females was significantly lower than those of virgin females ($t = 2.20$, $p < 0.05$) and those of 64-day mated females ($t = 2.23$, $p < 0.05$), while the difference between mated and virgin females under this temperature regime was not significant ($t = 0.02$, $p = 0.97$). By contrast, the mating scenario at 23 °C fluctuating, 23 °C constant, and 20 °C constant temperature regimes did not influence the total number of eggs laid by *A. proletella* females ($F = 1.4$, $p = 0.25$; $F = 0.08$, $p = 0.92$; and $F = 0.38$, $p = 0.68$ respectively).

The total number of eggs laid by *A. proletella* under the 20 °C fluctuating temperature regime was significantly higher than those under the 20 °C constant regime ($z = 2.14$, $p < 0.05$). Moreover, *A. proletella* was significantly more fecund under the 20 °C fluctuating temperature regime than under that of 23 °C constant ($z = -2.16$, $P < 0.05$). However, there was no significant difference between 23 °C and 20 °C constant ($z = -0.15$, $p = 0.88$); 23 °C fluctuating and 23 °C constant ($z = -0.38$, $p = 0.69$); 23 °C fluctuating and 20 °C constant ($z = 0.26$, $p = 0.79$); 23 °C and 20 °C fluctuating temperature regimes ($z = -1.84$, $p = 0.06$) [figure. 4].

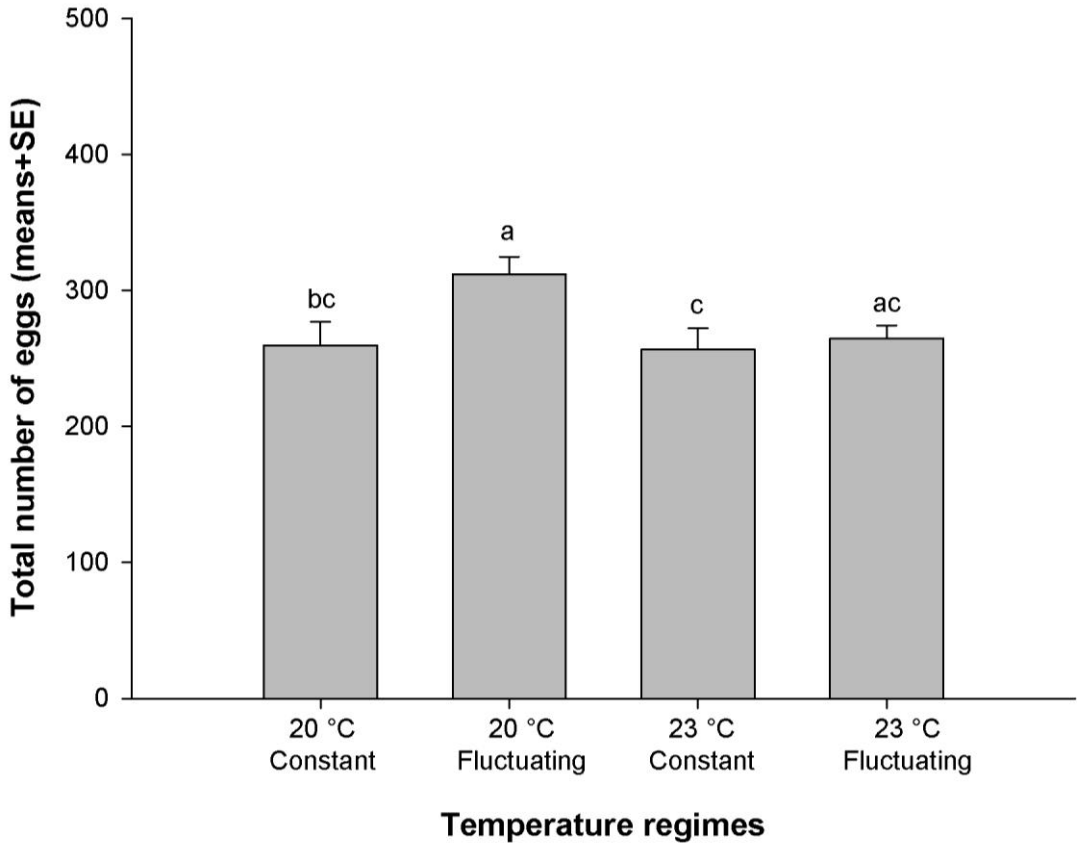

Figure 4: Total number of eggs of *A. proletella* under different temperature regimes (means + SD). Different letters indicate significant differences between temperature regimes. Generalized linear model (GLM) with quasi Poisson errors ($P < 0.05$).

Daily fecundity of *A. proletella*

Under the 20 °C fluctuating temperature regime, the daily fecundity of 64-day mated females was significantly higher when compared with the eight day mated females ($t = 2.34$, $p < 0.05$). However, there were no significant differences between virgin and 64-days mated females ($t = 0.5$, $p = 0.55$). Conversely, the mean daily fecundity of *A. proletella* did not significantly differ between virgin, 64-day and eight day mated females under the 23 °C fluctuating ($F = 0.68$, $p = 0.51$), 23 °C constant ($F = 0.67$, $p = 0.52$), and 20 °C constant temperature regimes ($F = 0.47$, $p = 0.62$).

We found a significantly higher mean daily fecundity under the 23 °C fluctuating temperature regime when compared to the 23 °C constant regimes ($t = -1.99$, $p < 0.05$), and 20 °C constant regimes ($t = 3.19$, $p < 0.05$). No significant differences were detected between the 23 °C fluctuating and 20 °C fluctuating ($t = 0.8$, $p = 0.38$); 20 °C

fluctuating and 20 °C constant (t = -1.77, p = 0.07); 20 °C fluctuating and 23 °C constant (t = -0.83, p = 0.40); 20 °C constant and 23 °C constant temperature regimes (t = 1.06, p = 0.29) [figure.5].

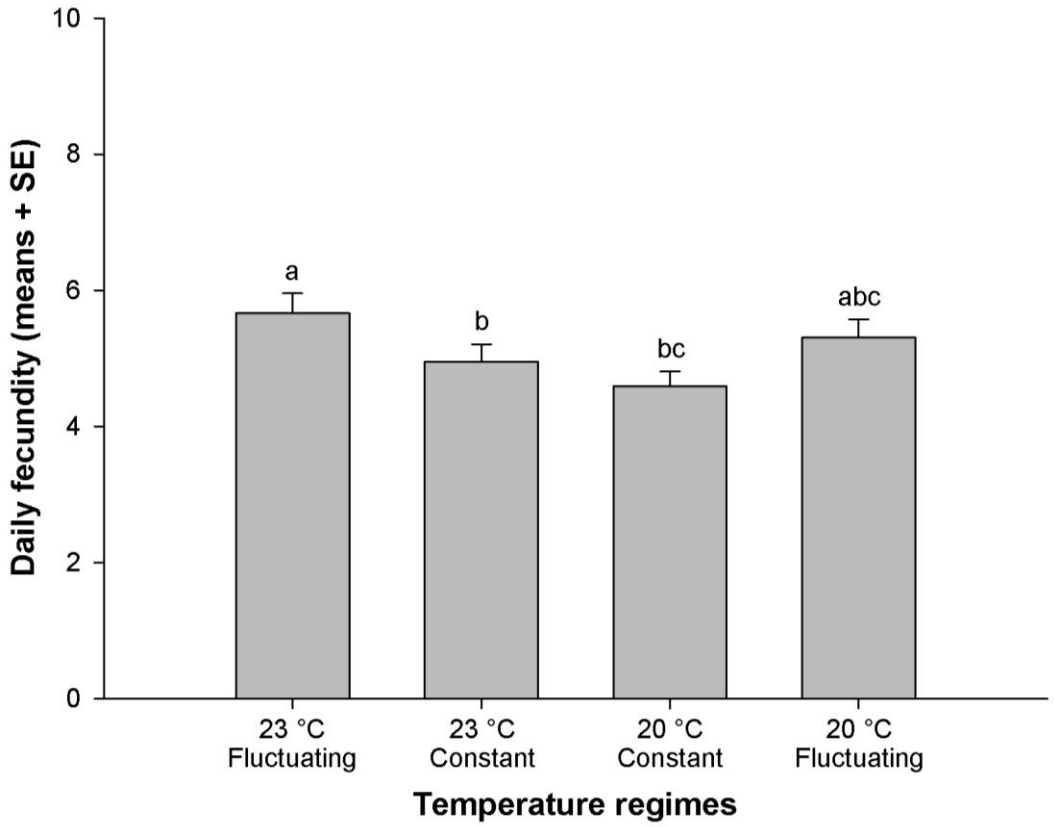

Figure 5: Daily fecundity of *A. proletella* under different temperature regimes (means + SD). Different letters indicate significant differences between temperature regimes (GLS, p < 0.05).

Age-specific fecundity of *A. proletella*

No significant overall effect of temperature under the 23 °C temperature regimes was found in terms of age-specific fecundity ($F = 1.21$, $p = 0.27$). However, a significant interaction between age and temperature regime was revealed ($F = 8.53$, $p < 0.001$) [Figure. 6].

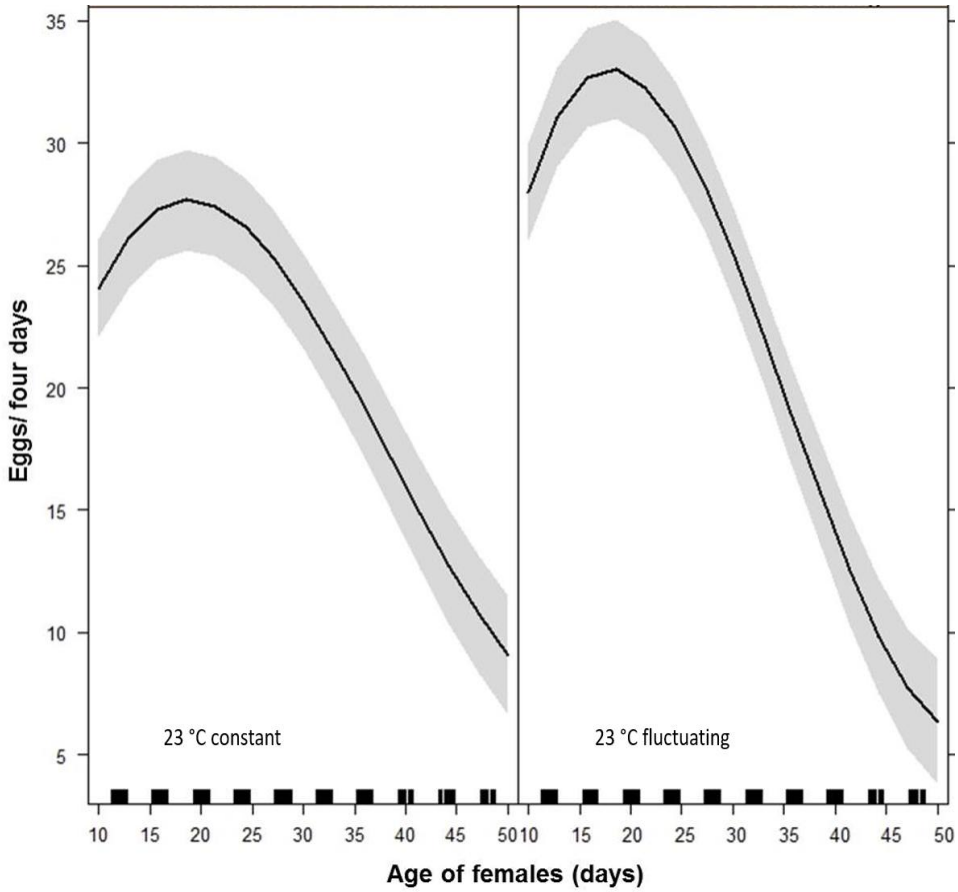

Figure 6: Age-specific fecundity (eggs/ female/ four days) of *A. proletella* under 23 °C fluctuating and constant temperature regimes. The curves were obtained from the mixed-effects polynomial model.

The 20 °C fluctuating temperature regime led to higher age-specific fecundity in comparison to the 20 °C constant temperature regime ($F = 4.17$, $p < 0.05$). Moreover, our model indicated that the interaction between temperature regime and age was also significant ($F = 3.08$, $p < 0.5$) [Figure. 7].

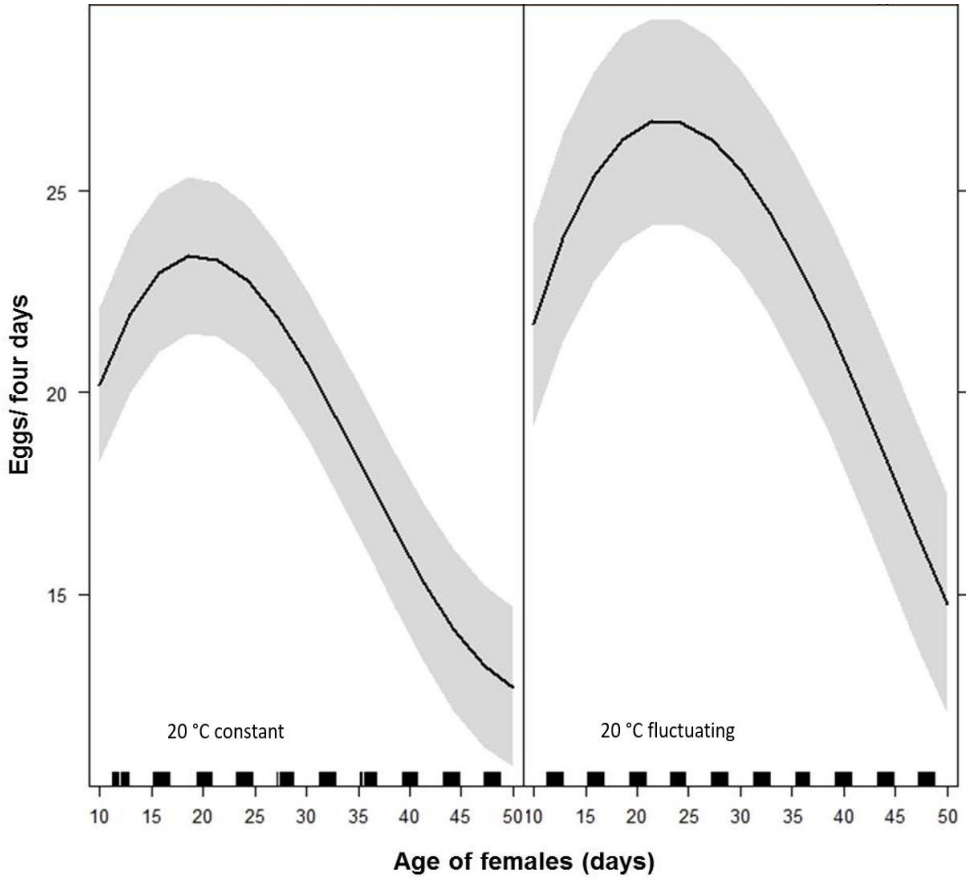

Figure 7: Age-specific fecundity (eggs/ female/ four days) of *A. proletella* under 20 °C fluctuating and constant temperature regimes. The curves were obtained from the mixed-effects polynomial model.

Effect of temperature regimes on sex ratio of *A. proletella*

Under all temperature regimes *A. proletella* 64-day mated females produced significantly more females (23 °C fluctuating = 70 %; 23 °C constant = 67 %; 20 °C fluctuating = 69 %; 20 constant = 64 %) than males (23 °C fluctuating = 30%; 23 °C constant = 33 %; 20 °C fluctuating = 31 %; 20 constant = 36 %) (Binomial test: 23 °C fluctuating: $p < 0.001$; 23 °C constant: $p < 0.001$; 20 °C fluctuating: $p < 0.001$; 20 °C constant: $p < 0.001$). Although the sex ratio of cabbage whitefly offspring under the 23 °C as well as the 20 °C fluctuating temperature regime was higher than those at the representative constant temperature mean, we did not find any significant differences between the different temperature regimes ($F = 0.90$, $p = 0.45$), [Figure. 8].

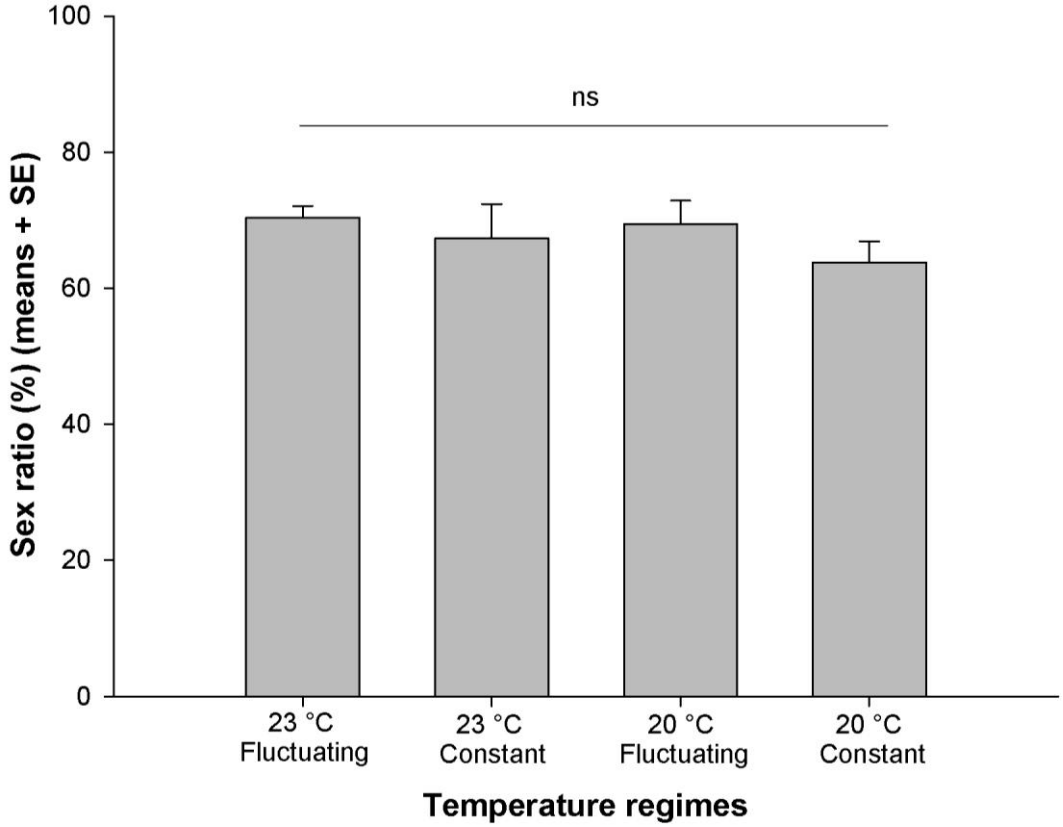

Figure 8: Effect of temperature regimes on the sex ratio of *A. proletella* offspring (%; mean + SD). Generalized linear model (GLM) with quasi-binomial distribution ($P < 0.05$); ns not significant.

Discussion

Despite the increasing importance of cabbage whitefly as a serious agricultural pest, few studies on the influence of temperature on its biological parameters have been performed to date. However, those studies that have been conducted have been based on constant temperature regimes. Body temperatures of ectothermic organisms are usually very close to those of the ambient environmental temperature. As a result, their metabolism can change in-line with temperature variation. Constant temperature regimes do not allow the metabolism of an insect to change as fluctuating temperatures do, which could in turn influence the fitness of an ectothermic organism. Despite the importance of these factors, this study reports, for the first time, the influence of fluctuating temperatures versus their equivalent constant means on the reproduction parameters of cabbage whitefly.

Survival rate:

We did not find any significant differences within the various temperature regimes between the survival rates of virgin, eight day mated, and 64-day mated female of cabbage whitefly. Similar behavior was reported in *B. tabaci*, in that the lifespan of the exotic B biotype reared on dwarf poinsettia (*Euphorbia* cyathophora Murray) did not differ between mated (23.4 days) and unmated females of 27.6 days (Barro and Hart, 2000). Conversely, Horowitz and Gerling (1992) demonstrated that *B. tabaci* multiple mated females had shorter lifespans than females that mated only once after emergence (10.4 days vs. 15.1 days). Our study demonstrated that mating history did not have any impact on the survival rate of cabbage whitefly males. Li et al. (2015) reported that the mating history of arrhenotokous *Thrips tabaci* males did not affect their survival rate. However, Partridge and Farquhar (1981) found that mating activity decreased the longevity of male fruit flies (*Drosophila melanogaster* Meigen). Our study did not find any significant differences within each temperature regime between the survival rate of *A. proletella* males and females. Salas and Mendoza (1995) reported identical lifespans of *B. tabaci* males (19.4 days) and females (19.0 days) on tomato plants (*Lycopersicon lycopersicum* L.) under laboratory conditions (25°C and

65% R.H.). Nevertheless, Powell and Bellows (1992) highlight that the lifespan of *B. tabaci* virgin females with 24.6, 15.5, 9.64, and 15.04 days was significantly higher than those of virgin males with 18.6, 12.23, 7.03, and 7.59 on cucumber plants (*Cucumzs sutivus* L., variety Poinsett 76) at different temperature regimes of 20, 25.5, 29, and 32 °C , respectively.

In the present study, we found that *A. proletella* adults exhibited different responses to temperature regimes. In detail, the survival rate of *A. proletella* females did not differ between fluctuating temperature and their constant mean. Nonetheless, we detected a significant difference between 20 °C constant and 23 °C fluctuating regimes, while the difference between 20 °C constant and 23 °C constant was not significant [Figure. 2].

We found that the survival rate of *A. proletella* males was significantly reduced by the fluctuating temperature regime. In this respect, the survival of males under the 23 °C fluctuating temperature was about 16 % towards the end of the experiment, whereas the survival rate of males at their representative constant mean was about 27 % [Figure. 3]. The survival rate of males (50 %) at the 20 °C fluctuating temperature towards the end of the experiment was lower than those at the 20 °C constant regime (78 %), but the difference was not significant. This could be explained through the concept that our experimental time (64 days) was not enough to detect the differences under such conditions. The reduced survival rate of males under fluctuating regimes versus the corresponding constant mean could be explained through the notion that fluctuating temperatures may be energetically demanding for males and therefore require a high metabolic rate. Accordingly, this cost in energy could be reflected as reduced survival rate in comparison to the constant temperature mean. Howe (1967) reported that the biological processes of an insect increase along with temperature. Another explanation could be that the 23 °C fluctuating temperature reached an unfavorable temperature for males, which could induce proteins that accelerate the aging process. There are no known comparable studies on the influence of fluctuating and constant temperature on the reproduction parameters of whiteflies. We therefore compared our results with studies on other insect species.

For instance, Davis et al. (2006) studied the effect of constant and alternating temperature on the green peach aphid, *Myzus persicae* (Sulzer), and reported that fluctuating temperature promoted the survival of the species compared to when kept at the comparative constant mean of (15 °C). However, this effect disappeared under moderate temperature conditions (20 °C fluctuating and constant temperature regimes). Joshi (1996) compared some biological traits of mosquitoes, *Aedes krombeini* (Huang), under fluctuating temperatures versus their constant means. He found that when mosquitoes were subjected to fluctuating temperatures, they lived longer than those subjected to the same constant means.

The significant differences detected in the survival rate of males, but not in females could mean that males are more sensitive to changing in temperatures than females. Cui et al. (2008) reported that the survival rates of *B. tabaci* females was higher than those of males when females and males were subjected to different heat-shock treatments.

Fecundity:

We found that mating for short periods of time under 20 °C fluctuating conditions reduced the fecundity of cabbage whitefly females in comparison to 64-day mated females. This shortage in fecundity could be explained through the notion that the eight day mated females reduced their fecundity in response to the exhaustion of stored sperm. However, this effect has become practically undetectable under the other temperature regimes. A possible negative effect of short mating periods on the oviposition of females has been examined in other insect taxa (Arnqvist and Nilsson, 2000). For instanc, French and Hammack (2011) reported that the multiple mated females of northern corn rootworm*, Diabrotica barberi* (Smith and Lawrence), oviposited more eggs than females that only mated once. The non-significant effect of mating scenario on the fecundity of cabbage whitefly under 20 °C constant, 23°C constant and fluctuating temperature regimes could be explained through the concept that the effects of mating scenario are not detectable under all conditions. This was also reported in other species, where the positive effect of multiple mating on the

longevity of the brunched beetle *callosobruchus maculatus* (Fabricius) was only noticeable under nutrient-stressed conditions (Fox, 1993).

The temperature regimes showed different responses in terms of the total number of eggs of cabbage whitefly. The total number of eggs deposited under the 20 °C fluctuating regime was significantly higher than those under the equivalent constant mean. Although the total number of eggs under the 23 °C fluctuating regime was higher than the corresponding constant one, this difference was not significant [Figure.5]. These results indicate that the 20 °C fluctuating temperature is likely to be the optimal body temperature for cabbage whitefly females. Accordingly, they maximized their oviposition under this temperature regime.

Davis et al. (2006) reported that *M. persicae* females produced at the best convenient constant temperature 5.9 offspring a week, while this production reached 12.2 offspring at the most favorable fluctuating temperature condition. The authors related this increase in the performance of this species under alternating temperature regimes to endosymbionts, which are likely to increase the amount of produced amino acids that in turn can enhance the fitness of this insect. Moreover, Auad et al. (2015) found that when *S. flava* aphids reared in climate chamber, that simulated the mean hourly temperature of an uncontrolled greenhouse, they had significantly more fecundity per female than aphids that lived under the constant temperature mean of 22.5 °C. Joshi (1996) compared the biological traits of mosquitoes, *A. krombeini*, under fluctuating versus their constant mean temperature regimes. He found that the fecundity values differ significantly between fluctuating and constant temperature conditions.

In the present study, fluctuating temperature affected the mean daily fecundity of cabbage whitefly, as shown by the higher mean daily fecundity under the 23 °C fluctuating temperature regime in comparison with the 23 °C constant temperature regime. Moreover, the shape of the age-specific fecundity curve at fluctuating regimes differ from those at constant temperature regimes (Figure. 6 and 7), resulting in a higher peak during the younger stages of the lifespan and a sharp decrease in oviposition as females become older. Similar behavior has been reported in other insect species. For instance, Mironidis and Savopoulou-Soultani (2008) found that the daily number of eggs of *Helicoverpa armigera* (Hübner) females reared under

fluctuating temperature regimes (25-10, 35-20, 35-27.5 °C) was higher than that of females reared under the corresponding constant means. Enkegaard (1993) investigated the influence of temperature on the biological parameters of the poinsettia strain of *b. tabaci*. Similar to our study, they found that females subjected to high temperatures reached a rapid and higher peak of age-specific fecundity when compared to those reared under lower temperature regimes. Moreover, a comparable behavior was also reported for *M. persicae* where the number of progeny per day was significantly increased under the fluctuating temperature compared to the corresponding constant temperature mean of 20 C° (Davis et al., 2006).

From another point of view, plant quality and food supply could also affect the reproduction parameters of an insect species. Biederbeck and Campbell (1973) found different soil microbial activities under fluctuating temperature regimes versus the corresponding constant means. As a result, the availability of nitrogen could be changed, which in turn could subsequently alter the quality of the plant. Jauset et al. (2000) reported that nitrogen fertilization not only changed tomato plants *Lycopersicon esculentum* (Miller), characteristics but it also influenced the reproduction of *T. vaporariorum* reared on the plants used. Fluctuating temperatures could therefore influence plant growth (Dale, 1964), which may affect the reproduction parameters of herbivorous insects.

Sex ratio

In this study, female adults were the predominant sex of *A. proletella* offspring by a significant margin, regardless of temperature regime. Despite the result that 64-day mated females reared under fluctuating temperatures tended to produce more females than those reared under constant temperatures, we did not find any significant influence of temperature regime on the sex ratio of *A. proletella* offspring. A similar female-biased sex ratio was also found for *A. proletella* that reared on different host plants (see chapter one). An increase in female sex ratio in-line with rising temperatures was also reported for *B. tabaci* that reared on poinsettia plants (*Euphorbia pulcherrima*), where the female ratio rose from 60 % at 19 °C to 76 % at 28 °C (Enkegaard, 1993). Powell and Bellows (1992) found that the sex ratio of *B. tabaci*

on cucumber plants (*Cucumis sativus* L.) increased with rising temperatures, for instance 50.2 % at 20 °C, 56 % at 25 °C, and 59.9 % at 30 °C. In addition, Gerling et al. (1986) reported that the sex ratio of *B. tabaci* changed depending on the season, being dominated by females in the spring and early summer and by males in the autumn. However, van Lenteren and Noldus (1990) summarized the findings of several studies and reported that the sex ratio of *T. vaporariorum* is likely to be even (1:1) and is not associated with temperature. Moreover, Cui et al. (2008) found that *T. vaporariorum* females that were exposed to different heat shock treatments were not influenced in terms of their sex ratio of the progeny.

Conclusion

In conclusion, this study shows that mating history could influence the fitness of cabbage whitefly under specific conditions. Interestingly, the difference in age-specific fecundity pattern, fecundity, and survival rate of males indicates not only that the fluctuating temperature regimes did not represent their corresponding constant mean, but also that fluctuating temperatures could be in favor of some aspects of the biological characteristics of cabbage whitefly. Therefore, our results suggest that all future estimating population dynamic models, as well as management strategies of *A. proletella*, should take all differences into account.

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Chapter 3

Life cycle and reproductive parameters of *Aleyrodes proletella* L. (*Hemiptera:* Aleyrodidae) in relation to mating scenario

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Abstract

Although the cabbage whitefly, *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae), has become a serious agricultural pest of *Brassicas* vegetables (*Brassica oleracea* L.), little information is known about its life history traits and population dynamics. For a more detailed understanding of its biology, we investigated development time, mortality of developmental stages, as well as the effect of mating scenario on fecundity, longevity, survival rate of Adults, and sex ratio under controlled conditions (temperature 20 °C, relative humidity 55-70 %, photoperiod: L16:D8) on Brussels sprouts (*Brassica oleracea var. gemmifera*). The different mating scenarios were, life span mated female and male, where the female and male *A. proletella* remained together throughout the experimental period, virgin female and male, and eight day mated female, where female and male were kept together for the first eight days of the experiment. The total life cycle from egg to adult was 28.93 ± 1.64 (mean ± SD) days. Egg mortality (7.6 %) was significantly higher than that of nymphs. The mating scenario did not significantly affect the life span and survival rate of males. The mating scenario did not significantly influence the longevity, survival rate or fecundity of *A. proletella* females. Virgin females produced male progeny only, whereas life span mated and eight day mated females produced female-biased sex ratio. However, the sex ratio of *A. proletella* offspring was significantly influenced by the duration of *A. proletella* male presence. The life span mated females produced significantly less female offspring than those of the eight day mated females 64 % and 71 %, respectively. The female-biased sex ratio and the similarity in longevity and fecundity for both eight day and life

span mated females suggest that *A. proletella* females do not need to mate frequently throughout their lifespan to optimize their reproduction parameters. These results could provide a better understanding of *A. proletella* population dynamics and growth, which will be helpful to develop control management strategies.

Keywords: *Aleyrodes proletella,* cabbage whitefly, development time, mating scenario, biological parameters.

Introduction

In the past, the cabbage whitefly, *Aleyrodes proletella* L. (Hemiptera: Aleyrodidae), was classified as a minor pest of several *Brassica* cultivars (*Brassica oleracea* L.) as well as related plants (Barro and Carver, 1997; Dale et al., 1976; Iheagwan, 1977; Martin et al., 2000). Nevertheless, it has increasingly become an important agricultural pest in many Europeans countries, e.g. United Kingdom (Springate and Colvin, 2012), Germany (Richter and Hirthe, 2014) and Spain (Muñiz and Nebreda, 2003), which has caused economical damage to the production of cabbage (*Brassica oleracea convar. capitata* L.), Brussels sprouts (*Brassica oleracea var. gemmifera DC*.), cauliflower (*Brassica oleracea var. botrytis* L.), kale (*Brassica oleracea var. sabellica* L.), kohlrabi (*Brassica oleracea var. gongylodes* L.), savoy cabbage (*Brassica oleracea convar. capitata var. sabauda* L.), and broccoli (*Brassica oleracea var. italica* Plenck) (Muñiz and Nebreda, 2003; Ramsey and Ellis, 1996; Richter and Hirthe, 2014; Schultz et al., 2010; Trdan et al., 2003; van Rijn et al., 2008). Moreover, Loomans et al. (2002) claimed that *A. proletella* has reached pest status on gerbera crops (*Gerbera jamesonii* L.) in green houses in the Netherlands.

The reasons for increasing problems of *A. proletella* reaching pest status are discussed controversially. Richter and Hirthe (2014) related the high population numbers to increased cultivation of oilseed rape (*Brassica napus* L.), which is considered to be a suitable habitat for overwintering of *A. proletella*. Mild winters and increasing temperatures are also likely to raise the survival of hibernating insects and enhance the growth of insect populations (Bale et al., 2002; Porter et al., 1991).

A. proletella originates from the European continent and is found worldwide (Dale et al., 1976; Evans, 2007; Martin et al., 2000). The species is a polyphagous phloem

sucker infesting a wide range of host plant species; with cruciferous plants considered to be the most important host plant family (Barro and Carver, 1997; Evans, 2007; Martin et al., 2000).

Adults are 1.5 mm in length, with four white wings marked with four gray spots (Byrne, 1991; Hill and Hill, 1994). Both body and wings are covered with a white powdery wax (Martin et al., 2000). The species is multivoltine, with more than three generations per year that overwinter on weeds (greater celandine *Chelidonium majus* L.), or overwintering cabbage crops such as winter cabbage and winter kale (Chen et al., 2007; Crüger and Backhaus, 2002; Iheagwan, 1977; Richter and Hirthe, 2014). Its developmental time from egg to adult depends on temperature and host plant (Alonso et al., 2009). Males and females develop through unfertilized and fertilized eggs, respectively (Byrne, 1991; Byrne and Devonshire, 1996). Eggs are laid in patches on the underside of leaves in a circular or semicircular pattern (Broekgaarden et al., 2012). After hatching, the neonate nymphs move short distances searching for suitable feeding sites (Bährmann and Moritz, 2002; Martin et al., 2000). Second, third, and fourth instar nymphs lose their ability to move and remain at the same feeding site throughout the developmental part of their lifecycle (van Emden, 2015). The nymphs grow by molting and finalize their development through pupation within the nymphal skin (Byrne, 1991; Hill and Hill, 1994).

Both adults and nymphs feed on plant sap and excrete honeydew, which is frequently colonized by black sooty molds (Hill and Hill, 1994). The presence of honey dew and mold fungi disturb plant photosynthesis and reduce plant growth (Martin et al., 2000). Additionally, plant quality and marketability are decreased by the presence of eggs, wax, nymphs, and honeydew (Mound and Halsey, 1978; Schultz et al., 2010).

The control of this species is a major challenge as adults and nymphs are hidden on the undersides of leaves. Conventionally, this pest is controlled by leaf applications of chemical insecticides (Springate and Colvin, 2012; Trdan et al., 2003). Repeated applications of these insecticides are needed to ensure total leaf coverage, eventually leading to resistant cabbage whitefly strains (Springate and Colvin, 2012). Recently, several biological control options were studied using predators (*Coccinella undecimpunctata* L., *Clitostethus arcuatus* Rossi) and parasitoids (*Encarsia tricolor*

Förster, *Encarsia inaron* Walker) (Cabral et al., 2006; Huang et al., 2009; Manzari et al., 2002; Mound and Halsey, 1978; Schultz et al., 2010; Williams, 1995).

Information about the specific life history traits of *A. proletella* is difficult to find and data on the basic biological parameters of this species is lacking. This study therefore aimed to fill the knowledge gap by providing detailed information on the biology of *A. proletella*, including developmental times of immature stages, live span, fecundity, sex ratio, and the influence of mating scenarios on reproduction parameters. A more comprehensive understanding of the population growth and population dynamics of *A. proletella* will contribute to refine management strategies of this pest species.

Material and methods

Whitefly source

Whitefly females of *A. proletella* were collected from Brussels sprout fields in Braunschweig (Lower Saxony, Germany; 52°16'N, 10°31'E) in October 2014. Five female adults were individually placed in rearing cages (60 × 60 × 60 cm) to obtain whitefly colonies that would harbor identical endosymbiont species. Adults were also reared on Brussels sprout plants (*Brassica oleracea var. gemmifera*). Consequently, whitefly clones were raised in a growth chamber at 20 °C and a photoperiod of L16:D8. Results of the identification of endosymbionts indicate that all colonies harbor identical secondary endosymbionts (P. Hondelmann, personal communication, April 15, 2015). One colony was chosen and all adults used in this experiment were sampled from this colony only.

Plant material

Brussels sprouts (*Brassica oleracea var. gemmifera* cv.Maximus, Syngenta, Germany) were used as test plants, which were grown in a green house in 14-cm plastic pots filled with potting compost (Klasmann-Deilmann, Geeste, Germany) at 16-20 °C and 50-75 % RH. Pots were fertilised two times a week with 0.01 % flory-1 (N-P-K-Mg 0.18-6-12-2, Gebr. Riege oHG, Germany) and watered as necessary. After two months, the plants were moved to a growth chamber and used for the experiments, fertilized and watered as described above.

Whitefly development and survival

Seven mated whitefly females (7-10 days old) were confined to the lower surface of the first fully grown leaves of Brussels sprout plants using clip cages (35×10 mm). The caged females were allowed to lay eggs for ten hours. Subsequently, adults were removed with an aspirator. Only ten eggs were chosen at random, and all remaining eggs were removed. After the eggs had hatched and the first instar had settled down, each location of the first larvae was marked and numbered. The larvae were examined under a microscope daily (Zeiss, Stemi sv8, Germany) to determine their development and emergence rates. Instars were identified according to their body size and the presence of molting skin. Seven replicates were used in this experiment and the mean total development time was calculated from whitefly adults that successfully completed their development. Plants were kept in growth chambers at 20 °C and 50-70 % relative humidity, with a photoperiod of L16:D8.

Reproductive parameters

1. Obtaining of one-day old adults

In order to obtain one day old virgin females and males of *A. proletella*, adults were transferred to clip cages attached to the lower side of fully grown leaves of Brussels sprout plants (15 adults in each cage). Plants were kept in a growth chamber at 25 °C with a photoperiod of L16:D8. Females were allowed to lay eggs for 24 hours. Subsequently, all adults and clip cages were removed. Later on, to insure virgin adults, red eye pupae were transferred to small Petri dishes (35×10mm) using a needle (one pupa per Petri dish) one day before adult emergence. The Petri dishes were filled with small pieces of Brussels sprout leaves placed on wet filter paper. Adults that hatched within 15 h were considered to have the same age (one day old). The sex of newly emerged adults was determined under a microscope (Zeiss, Stemi sv8, Germany) with the help of a modified mouth aspirator.

2. Measuring of fecundity and longevity

To monitor the fecundity and longevity of the whitefly, clip cages were attached to the lower surface of the tenth fully grown leaf of each plant (the numbering of leaves started with the youngest full grown leaf). Thereafter, the following treatments were set up: a) Life span mated females (LMF) and males (LMM): in this treatment, females and males were kept together throughout the experimental period. b) Eight day mated females (8MF): where females and males were kept together for the first eight days, after which the males were removed. c) Virgin females (VF): unmated females were kept alone throughout the experimental period. d) Virgin males (VM): unmated males were kept alone throughout the experimental period. At four day intervals, adults and clip cages were transferred to new leaves, i.e. the next younger leaf on the same experimental plant. Thereafter, the number of eggs was recorded using a microscope (Zeiss, Stemi sv8, Germany) and new clip cages were again placed on the leaves in the same position. Additionally, the survival rate of adults was recorded daily. This experiment was finished when all adults (females as well as males) were dead. The experiment was designed as a random block design with ten replicates. The experiment was carried out in a growth chambers at 20 °C and 50-70 % relative humidity, and a photoperiod of L16:D8.

3. Sex ratio

Every seven days, following the transfer of adults to new leaves, all infested leaves were excised and the petioles were transferred to glass tubes filled with water and kept in the same growth chamber (at 20 °C, relative humidity of 50-70 % and a photoperiod of L16:D8). After adult emergence, leaves with clip cages were placed in a deep freezer at -16 °C to kill the adults. The sex ratio of the adults was then determined using a microscope (Zeiss, Stemi sv8, Germany).

Statistical analysis

Data was analyzed using the R statistical program version 3.2.3 (R Core Team, 2016)

Differences between the mortality of egg and nymph stages were analyzed using the Kruskal-Wallis Test. Due to the similar mortality between different nymphal stages, mortality was compared only between the eggs and the first instars.

Adult longevity was analyzed using the linear model function (lm) with Adult longevity as the dependent and treatments as the independent variable (R Core Team, 2016). Longevity data was transformed with the Box-Cox power transformation using the MASS package to meet normality (Venables and Ripley, 2002). To detect the influence of mating scenario on the survival rate of cabbage whitefly adults, the Kaplan-Meier survival analysis (log-rank test) was performed (Therneau and Grambsch, 2000).

In order to analyze the fecundity, generalized linear models (GLM) were fitted with quasi Poisson errors (R Core Team, 2016). Total fecundity was used as the dependent variable and treatments as the independent variable.

To determine whether the mating scenario influenced the sex ratio of the progeny, males and females were grouped together as the response variable and analyzed using the general linear model with quasi binomial errors (Crawley, 2013). Additionally, binomial tests were performed to determine whether the sex ratio of cabbage white flies departed from the even sex ratio of 50:50 (Crawley, 2013)

All previous general Linear models (GLM) that were used have shown no obvious pattern when the residuals were plotted against the fitted values.

Results

Development time

The mean development times of eggs, first to fourth instars and pupa were (mean ± SD) 9.85 ± 0.057, 4.19 ± 0.22, 2.86 ± 0.10, 3.63 ± 0.06, 4.76 ± 0.10, and 3.97 ± 0.06 days, respectively. The mean total development time of *A. proletella* was about 28.93 ± 0.28 days for the rearing conditions used in the experiment [Figure.1]. The mortality of eggs was significantly higher with 7.6 ± 3.19 % compared to those of the instars with zero % (x^2 = 5.09, p = 0.024) [Figure.1].

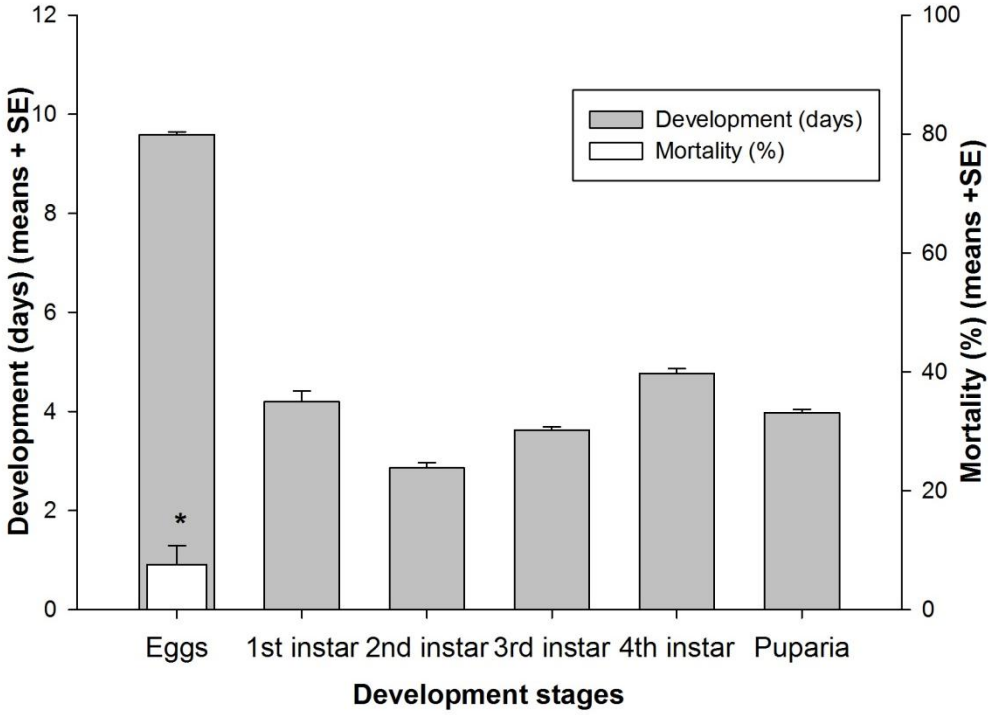

Figure 1: Development duration in days (means + SD) and mortality (%; mean + SD) of different development stages of *A. proletella*. Asterisks (*) indicate significant differences between treatments according to Kruskal-Wallis Test (P < 0.05).

Adult longevity

Life span did not significantly differ between the whitefly adults for all treatments tested (F = 1.2, P = 0.31). The mean longevity of virgin females, life span mated females, eight day mated females, virgin males, and life span mated males was about 67.8 ± 5.07, 64 ± 5.28, 71 ± 6.04, 82 ± 6.00, and 68 ± 8.48 days, respectively [Figure.2]. In addition, the mating scenario also did not affect the survival rate of *A. proletella* females (log-rank test: x^2 = 1.4, p = 0.48) [Figure.3].

The survival rate of virgin males did not significantly differ from that of the life span mated males (log-rank test: x^2 = 1.8, p = 0.17) [Figure.4].

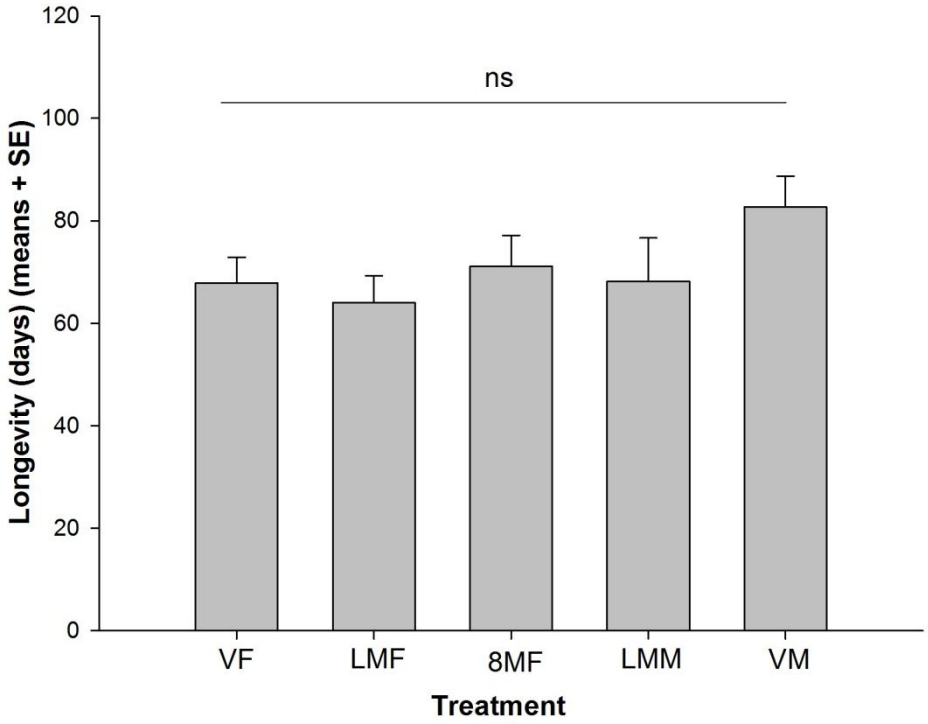

Figure 2: Effect of mating scenarios on total longevity of *A. proletella* adults. Treatments: LMF: Life span mated females; 8MF: Females mated for eight days; VF: Virgin females; VM: Virgin males; LMM: Life span mated males ANOVA (P < 0.05); ns: not significant.

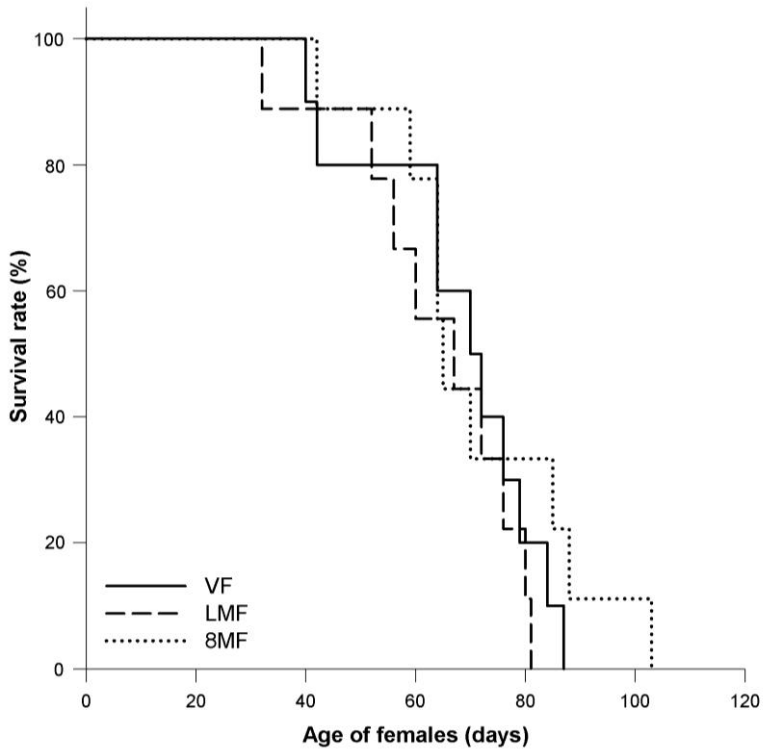

Figure 3: Survival rate of *A. proletella* females in different treatments. Treatments: LMF: Life span mated females; 8MF: Females mated for eight days; VF: Virgin females. log-rank test ($P < 0.05$).

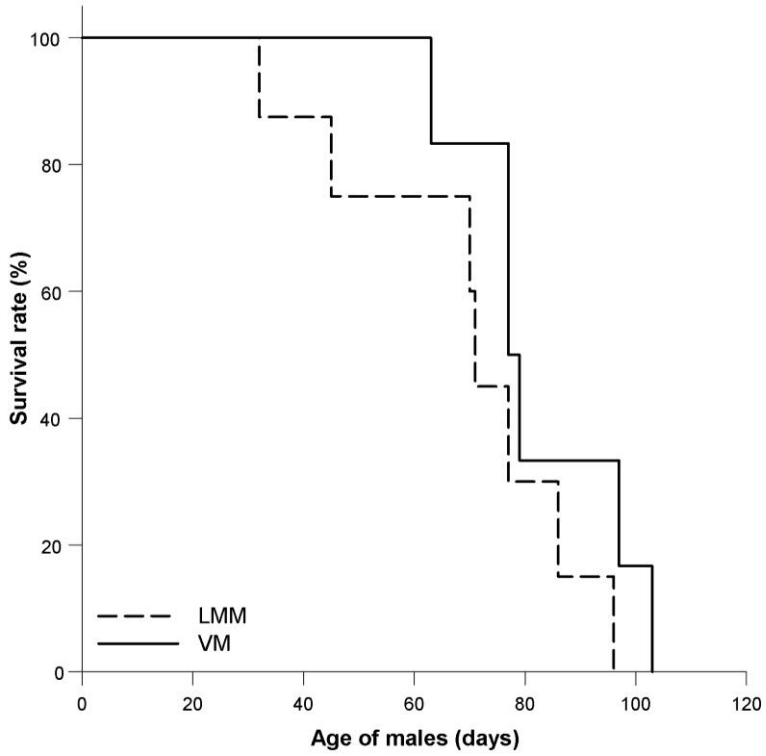

Figure 4: Survival rate of *A. proletella* males in different treatments. Treatments: VM: Virgin male, LMM: Life span mated males. log-rank test ($P < 0.05$).

Effect of mating on fecundity

The fecundity of virgin females (284 ± 31.52 eggs) as well as that of life span mated females (283 ± 33.51 eggs) was slightly, but not significantly (F = 0.36, p = 0.69), higher than that of eight day mated females 250 ± 30.89 [Figure. 5].

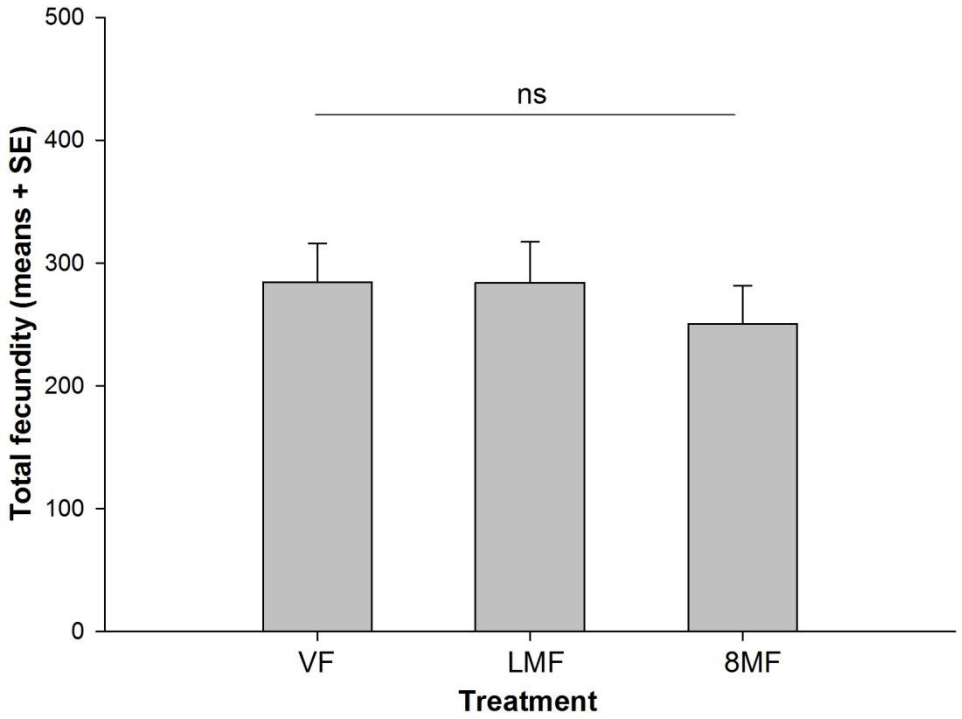

Figure 5: Effect of mating scenarios on total fecundity of *A. proletella* (means +SD). Treatments: LMF: Life span mated females; 8MF: Females mated for eight days; VF: Virgin females. Generalized linear model (GLM) with quasi Poisson errors (P < 0.05); ns: not significant.

Effect of mating scenarios on Sex ratio

The sex ratio of whiteflies at 20 °C significantly differed from an even sex ratio (50:50). Both, life span mated females and eight day mated females produced significantly more female (FM = 64 %; 8MF = 71 %) than male (MF = 36 %; 8MF = 29 %) whiteflies (binomial test: FM, p < 0.001; 8MF, P < 0.001). The sex ratio of *A. proletella* offspring was significantly influenced by the mating treatment (b = 0.36, SD = 0.14, t (16) = 2.50, P < 0.05). The eight day mated females produced significantly higher female offspring than those of the life span mated females [Figure. 6]. One hundred percent of unmated females gave birth to male flies.

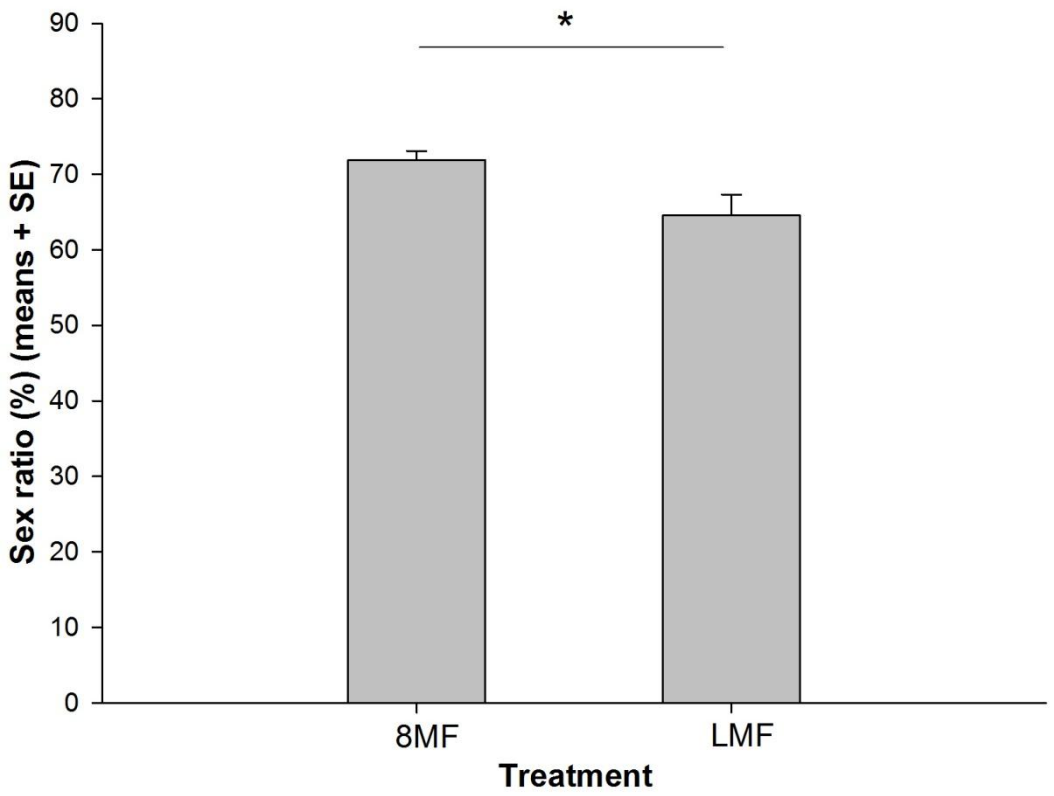

Figure 6: Effect of mating scenarios on sex ratio of *A. proletella* (%; means + SD). Treatments: LMF: Life span mated females; 8MF: Females mated for 8 days. Asterisks (*) indicate significant differences between treatments according to generalized linear model (GLM) with quasi binomial distribution ($P < 0.05$).

Discussion

Despite increasing damage caused by the cabbage whitefly, information on life history traits of this species remains limited. A more detailed understanding of the biology of this insect pest could contribute to the development of more refined control management strategies.

Development time

In this study, the entire life cycle (egg-adults) of *A. proletella* reared on Brussels sprouts was nearly equal to that reported by Alonso et al. (2009), i.e. 28.5 days, on broccoli at the same temperature regime of 20 °C. However, other studies have reported that both host plant and temperature influence the developmental time of *A. proletella* (Campos et al., 2003; Iheagwan, 1978; Nebreda et al., 2005).

The survival of cabbage whitefly nymphs on Brussels sprout plants has not been studied in detail. So far we found that the survival of eggs was significantly lower than that of nymphs, given the specific conditions in our experiments. While the nymphs completed their development with a 100 % survival rate, the eggs finalized their development with a 7.6 % mortality rate. Similar high survival rates of immature *A. proletella* ranging from 73 to 100 % were reported by Alonso et al. (2009) on broccoli at different constant temperatures (16, 18, 20, 22, 24, 26, 28, and 30 °C). Lin and Ren (2005) reported high survival rates for the first, second, and fourth development stages (100 %) of *Bemisia tabaci* (Gennadius) on cotton rose hibiscus (*Hibiscus mutabilis* L.). Nava-Camberos et al. (2001) reported similar survival rates (100 %) for *Bemisia argentifolii* (Bellows & Perring) for all development stages when *B. argentifolii* was reared on cantaloupe (*Cucumis melo var. cantalupensis*) at 20 °C. Based on information from other whitefly species, the mortality of whitefly developmental stages could be influenced by the host plant (Kakimoto et al., 2007), host leaf age (Zhang and Wan, 2012), nitrogen fertilization (Bentz et al., 1995), and temperature (Mansaray and Sundufu, 2009; Nava-Camberos et al., 2001).

Lifespan and survival

In this study, the life span of cabbage white fly adults on Brussels sprout plants was seven to ten times higher than what was reported by El-Helaly et al. (1972) on cauliflower (*Brassica oleracea var. botrytis* L.) at 16 °C, who noted the life spans of mated females, virgin females and mated males to be 12.4, 7.4, and 7.8 days, respectively. Differences in temperature regimes, host plant species, methods used, and techniques between these studies could contribute to the variance in results.

We did not find any significant differences between the life span of differently treated males and females of *A. proletella*. Similar longevity of males (19.4 days) and females (19.0 days) was also reported for *B. tabaci* adults on tomato plants (*Lycopersicon lycopersicum* L.) under laboratory conditions of 25 °C and 65 % R.H. (Salas and Mendoza, 1995). However, Khan and Wan (2015) found that the females of *B. tabaci* lived slightly longer than males. Furthermore, Powell and Bellows (1992) reported that the longevity of *B. tabaci* females with 15.5, 9.64, and 15.04 days was significantly higher than those of males with 12.23, 7.03, and 7.59 days on cucumber plants (*Cucumzs sutivus* L.) at the temperature regimes of 25.5, 29, and 32 °C, respectively. Moreover, Campos et al. (2003) reported that the life span of *Trialeurodes vaporariorum* (Westwood) females reared on different bean (*Phaseolus vulgaris* L.) cultivars is likely to be slightly greater than that of males at 23 °C.

We also demonstrated that the mating treatments did not have any effect on the survival rate of the cabbage whitefly adults. Moreover, the non-significant effect of mating scenario on the longevity of virgin, eight day, and life span mated females indicated that the mating activity did not influence the reproduction parameters of *A. proletella* females in terms of increasing or decreasing their life span. De Barro and Hart (2000) did not find any differences in the longevity between mated and unmated females of indigenous and exotic biotypes of *B. tabaci*. However, Horowitz and Gerling (1992) found that multiple mated *B. tabaci* females lived shorter than those that only mated once after emergence, 10.4 and 15.1 days, respectively.

Although the virgin males lived longer (82 ± 6.00 days) than the mated males (68 ± 8.48), the cost of sexual activity in terms of a decreased longevity was not significant in

our study. Possible negative effects of mating history on the longevity of males have been reported in other taxa. For instance, Cordts and Partridge (1996) reported that mating activity decreased the longevity of fruit fly males *Drosophila melanogaster* Meigen. Moreover, the lifespan of male *Saltella sphondylli* was also negativity affected by mating frequency (Martin and Hosken, 2004).

Fecundity

Neither the absence of males nor the duration of *A. proletella* male presence significantly influenced the fecundity of *A. proletella* [Figure. 5]. In this respect, the total number of eggs of eight day mated females tends to be slightly, but not significantly, lower than those of virgin and life span mated females. The assumption that mating could be costly or beneficial for females in terms of increasing or decreasing their total fecundity was not detectable in this investigation. This is in line with Omondi et al. (2005), who reported similar numbers of eggs laid by virgin (8.64 eggs) and mated females (9.56 eggs) of cassava biotypes of *B. tabaci* on eggplant *Solanum melongena* L.. De Barro and Hart (2000) also reported that the daily fecundity of indigenous eastern (EAN) biotypes of *B. tabaci* did not differ between mated and non-mated females with 10.31, and 9.31 eggs, respectively. Horowitz and Gerling (1992) demonstrated that the total number of eggs laid per multiple mated females of *B. tabaci* did not differ from those that mated only once after emergence. Although, the cost or benefit of mating scenario could not be seen in our study, those that investigated other insects taxa demonstrated that mating history could positively or negatively influence the fecundity of some insects (Arnqvist and Nilsson, 2000; Li et al., 2015).

Sex ratio

We found that the sex ratio of *A. proletella* offspring was significantly influenced by the presence of males. While females that were able to mate throughout their life span produced 64 % female offspring, females that mated for eight days produced 71 % female offspring, which was significantly higher than the former female ratio. This result could be explained by the reduced fecundity in females that mated for eight days (250 compared to 283 eggs in those were able to mate throughout their life

span). This could be a response to the depletion of stored sperm leading to a subsequent decrease in the proportion of males to only 29% compared to 36% in life span mated females.

In contrast to our study, Van Lenteren and Noldus (1990) reported that the sex ratio of other whitefly species (*T. vaporariorum* and *B. tabaci*) tends to be even (50:50). However, Omondi et al. (2005) reported a 68 % female sex ratio of cassava biotypes of *B. tabaci* on eggplant. Cui et al. (2008) found a 53.0 to 55.2% female sex ratio of *T. vaporariorum* on green bean plants *Phaseolus vulgaris* L. under different heat shock treatments. Tsueda and Tsuchida (2011) claimed that mating between different biotypes of *B. tabaci* could influence the sex ratio of whitefly. Another parameter that may influence sex ratio is the host plant (Qiu et al., 2011). In this study, the virgin females produced only males. These observations are similar to those reported for other whitefly species (Byrne and Devonshire, 1996). Horowitz and Gerling (1992) investigated the sex ratio of *B. tabaci* females that mated only once after emergence, compared to females that mated throughout their life time. In contrast to our study, they found that the presence of males increased the production of female in the progeny.

The similar longevity, fecundity and female-biased sex ratio for both eight day and life span mated females suggest that mating for short periods over of lifetime could be sufficient for *A. proletella* females to optimize their reproduction parameters. A behavior that has also been documented in other insects studies (Fox, 1993; Kakimoto et al., 2007; Li et al., 2015; Ridley, 1988; Walker, 1980). Further investigation into the biology of cabbage whitefly, will help to understand their reproduction potential, and to develop cabbage whitefly-specific management strategies.

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General discussion

Exploring the biological traits of a herbivore insect species is considered to be of a great importance to understand the population dynamics and develop sufficient management strategies to control this insect species. Historically, the cabbage whitefly was known as a non-significant pest of *Brassica* crops. Accordingly, it gained little attention and its biology was understudied. However, this species has recently gained more importance, as a key *Brassica* crops pest, and is today classified among the most destructive insect pests that threaten *Brassica* crop production. Due to a lack of knowledge on its biology, as well as the reasons behind the current outbreak, it can be argued that current management programs have not worked effectively. To tackle the knowledge gaps on the basic biology of cabbage whitefly, we investigated the influence of different host plants, temperature regimes, and mating scenarios on its basic biological traits and population dynamics. Gaining such information about the biological traits of this insect pest could contribute towards understanding the reasons behind the current population growth and the development of management strategies to control this pest.

In the present study we found that the pre-oviposition period of *A. proletella* was affected by the host plant where the highest and the lowest pre-oviposition period was detected on winter oilseed rape (1.61 ± 0.1 days) and cabbage (2.61 ± 0.27 days), respectively. This could be explained through the assumption that the structure and nutrient components of winter oilseed leaves were in favor of young cabbage whitefly females. It has been shown that components and structure of plant leaves have an effect on the fitness of cabbage whitefly (Broekgaarden et al., 2012; Loomans et al., 2002; Ramsey and Ellis, 1996). In addition, Qiu et al. (2011) investigated the influence of different host plants on the performance of the B biotype and Cv biotype of *B. tabaci*. Similar to our results, they reported that the pre-oviposition period of both biotypes was affected by the host plant.

On the other hand, we found a significantly higher daily fecundity on winter oilseed rape (9.07 eggs) in comparison to kale (7.56 eggs), kohlrabi (6.11 eggs), and cabbage (5.00 eggs). Also, the age-specific fecundity was the highest on winter oilseed rape and

the lowest on white cabbage. In a previous study, the highest daily fecundity of cabbage whitefly was reported on late cauliflower *Brassica oleracea* L. variety 'botrytis' cultivar Picasso (4.7 eggs) (Nebreda et al., 2005). The differences in performance of cabbage whitefly in terms of fecundity on different host plants could be related to leaf characteristics. Accordingly, Ramsey and Ellis (1996) reported that the thick leathery leaves of *Brassica cretica and Brassica insularis* are likely to negatively affect the oviposition of cabbage whitefly.

Another impact of host plants on the biology of whitefly was detected on the survival rate of females and males. In this respect, the lowest survival rates of female and males were detected on white cabbage while the highest survival rates were found on winter oilseed rape as well as on kohlrabi. This finding corresponds to Broekgaarden et al. (2012) who found that the *A. proletella* adults were able to survive for a short time on white cabbage (*B.oleracea capitate var. alba*) cultivar Rivera. More interestingly, we found that the host plant significantly affected the sex ratio of *A. proletella* progeny. In this respect, the highest female ratio was found in winter oilseed rape (70 %) and kale (75 %) whereas the lowest was fund on kohlrabi (64 %) and cabbage (64%). Similarly, Huang et al. (2014) found that the host plant significantly influenced the sex ratio of the castor whitefly *Trialeurodes ricini* (Misra). Furthermore, Omondi et al. (2005) reported that the sex ratio of the okra biotype of *B. tabaci* was associated with the host plant.

To gain a more comprehensive understanding of the effect of temperature on the biology of cabbage whitefly, we compared the performance of whitefly adults under different fluctuating and constant temperature regimes. Our results indicate that the survival rates of *A. proletella* females were significantly affected by the temperature regime, where the lowest survival rates were observed under 23 °C fluctuating temperature and the highest were observed under 20 °C constant and fluctuating temperature regimes. A similarly significant effect of the temperature regime was also observed in the survival rate of males. In detail, the survival of males at 23 °C fluctuating temperature was significantly lower than those at a 23 °C constant, 20 °C fluctuating, and 20 °C constant temperature regime. This indicates that the fluctuating temperature did not represent their equivalent constant mean at the 23 °C

temperature regime. Similar behavior was also reported by Davis et al. (2006) for the green peach aphid, *Myzus persicae* (Sulzer), as the study found that the survival rate of the green peach aphid maintained at a 15 °C fluctuating temperature did not represent their equivalent constant mean. Auad et al. (2015) found that the longevity of aphids *Sipha flava* (Forbes) at fluctuating temperature was longer than those that lived under the same equivalent constant temperature mean. Also, we found that the oviposition of *A. proletella* females exhibited different responses to temperature regimes. The main interesting difference was found between 20 °C fluctuating and 20 °C constant temperature regimes, in that the 20 °C fluctuation regime significantly increased the total fecundity of the cabbage whitefly females. Another difference was also detected on the shape of the age-specific fecundity curve where the shape of the curve obtained at fluctuating regimes did not reflect those obtained at constant temperature regimes. Davis et al. (2006) studied the performance of the green peach aphid, *M. persicae*, under alternating and constant temperature regimes. Similar to our results, they reported that the reproduction of green peach aphids was the highest under alternating temperature regimes. The authors linked this increase in the reproduction to the increasing performance of endosymbionts, which support aphid with amino acids. Moreover, Joshi (1996) reported that the oviposition of mosquitoes, *Aedes krombeini* (Huang), differed significantly between fluctuating and constant temperature regimes.

On the other hand, the sex ratio of cabbage whitefly in this study was significantly in favor of females. However, the temperature regimes had no influence on the sex ratio of cabbage whitefly. This finding corresponds to van Lenteren and Noldus (1990) who reported that the temperature did not influence the sex ratio of *T. vaporariorum*. By contrast, Powell and Bellows (1992) claimed that the sex ratio of *B. tabaci* on cucumber plants (*Cucumis sativus* L.) increased with increasing temperatures.

To gain more knowledge and understand further aspects of the biological characteristics of cabbage whitefly, we investigated the influence of mating history on the fecundity, life span, survival rate, and sex ratio of this insect species. The mating scenario did not significantly affect the pre-oviposition period of cabbage whitefly. The mated and unmated females started to oviposit at the same time after emergence. By

contrast, El-Helaly et al. (1972) found that Pre-oviposition period of virgin females tended to be slightly higher than those of mated females.

Our findings indicate that the survival rate of *A. proletella* adults reared under different temperature regime conditions or those reared on different host plants was not associated with the mating scenario. The life span of *A. proletella* adults was also not affected by the mating history. This is in line with Barro and Hart (2000), who found a similarly long lifespan between mated and unmated *B. tabaci* females. By contrast, Horowitz and Gerling (1992) found that multiple mated *B. tabaci* females lived longer than females that mated shortly after emergence. Moreover, the longevity and survival rate of females did not differ significantly from those of males. Salas and Mendoza (1995) did not find significant differences between the life span of males and females of *B. tabaci*. However, Powell and Bellows (1992) reported that the life span of *B. tabaci* females was significantly higher than those of males.

In all experiments, the mating scenario did not affect the fecundity of *A. proletella* females, except under 20 °C fluctuating temperature regimes where the fecundity of eight day mated females was significantly lower than that of virgin and 64-day mated females. Barro and Hart (2000) reported that the fecundity of *B. tabaci* virgin females did not differ from mated females. We also demonstrated that the mating treatments significantly influence the sex ratio of cabbage whitefly. In detail, females that were able to mate throughout their life span produced 64 % female offspring, whereas females that mated for eight days produced 71 % female offspring. However, in this study, virgin females only produced male progeny. There is no data to compare our results with, as research has until now failed to investigated the sex ratio of cabbage whitefly.

In conclusion, this study shows that a) winter oilseed rape is a susceptible host plant for the cabbage whitefly, which supports the hypothesis that the increasing cultivated areas of oilseed rape could be one of the reasons for the current outbreak of cabbage whitefly. b) The fluctuating temperature regime did not represent their equivalent constant mean, which indicates that laboratory experiments under constant temperatures might not be able to reflect what happens in nature. c) The female-biased sex ratio and similar life span and survival rate of short period mated females

and life span mated females indicate that mating for short period of time after emergence is likely to be sufficient for *A. proletella* females to reach their optimal reproduction parameters. Further studies on the biology of cabbage whitefly could help to discover the reasons behind its current population growth and subsequently to optimize their management strategies.

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E r k l ä r u n g e n

1. Hiermit erkläre ich, dass diese Arbeit weder in gleicher noch in ähnlicher Form bereits anderen Prüfungsbehörden vorgelegen hat.

   Weiter erkläre ich, dass ich mich an keiner anderen Hochschule um einen Doktorgrad beworben habe.

   Göttingen, den .....

   .....

   (Unterschrift)

2. Hiermit erkläre ich eidesstattlich, dass diese Dissertation selbständig und ohne unerlaubte Hilfe angefertigt wurde.

   Göttingen, den .....