INTRODUCTION

Millions of US dollars of crop loss per year are attributed to thrips feeding (Lewis, 1973, 1997). The 1–3 mm long insects damage plants by piercing and sucking out cell contents of leaves, flowers and fruits. Additionally, a few species of thrips are propagative vectors of plant viruses, for example Tospoviruses. They also transmit other viruses in a non-propagative manner (members of Machlomovirus, Ilarvirus, Carmovirus, Sobemovirus), as well as other pathogens, such as bacteria and fungi (Gitaitis, Walcott, Wells, Diaz Perez, & Sanders, 2003; Jones, 2005; Ullman, Sherwood, & German, 1997). Their adaptability to different environmental conditions, cryptic lifestyle, ability to develop broad insecticide resistance (www.pesticideresistance.org; 10 species listed, 9th July 2019), and constraints related to their detection in traded host crop products, have resulted in a worldwide spread of many pest species. Hence, new approaches for thrips...
management are needed. The use of thrips semiochemicals offers the potential for a more effective monitoring and optimization of their control (Hamilton & Kirk, 2003; Kirk, 2017; Teulon et al., 2017).

Several semiochemicals of thrips are known, often functioning as alarm pheromones or defensive allomones (Moritz, 2006). Some have shown potential in enhancing effects of insecticides, for example against Frankliniella occidentalis larvae (Cook, Dadour, & Bailey, 2002; MacDonald, Hamilton, Jacobson, & Kirk, 2002). Other pheromones, such as aggregation or sex pheromones, have been identified only from six male thrips species (Echinothrips americanus, Krueger, Moritz, Lindemann, Radisch, & Tschuch, 2016; Frankliniella intonsa, Zhang, Zhu, & Lu, 2011; Frankliniella occidentalis, Hamilton, Hall, & Kirk, 2005; Kirk & Hamilton, 2010; Olaniran et al., 2013; Frankliniella schultzei, Milne, Walter, & Milne, 2002; Thrips palmi, Akella et al., 2014; Kirk & Hamilton, 2010; Megalurothrips sjostedti, Niassy et al., 2019).

In male E. americanus, two dibasic esters (dimethylglutarate DBE-5 and dimethyladipate DBE-6) were found, which function as an antiaphrodisiac and male recognition pheromone (Krueger et al., 2016) and might have potential in mating disruption (Kirk, 2017).

Echinothrips americanus has spread around the world within the last 20–30 years (Andjus, Jovic, & Trdan, 2009; Collins, 1998; Ferguson & Ship, 2002; Itoh, Oguri, & Suzuki, 2003; Mirabal-Balou, Lu, & Xue-Xin, 2010; Mound, 2000; Mound et al., 2013; Mound & Ng, 2009; Shipp, Gillespie, Fry, & Ferguson, 2001; Varga & Fedor, 2008; Vierbergen et al., 2006). This invasiveness, together with its phytophagous lifestyle and broad host range of about 24 plant families (Vierbergen, 1998) mean that E. americanus, has the potential to become a major pest.

This arrhenotokous species produces female progeny by fertilized eggs, whereas unfertilized eggs result in males only (Krueger, Mound, & Moritz, 2015; Kumm, 2002; Li, Zhang, & Feng, 2012). Additionally, this species regulates the larval development of its progenies in relation to the mating status of the mother and contact with other individuals. Mothers with limited or no access to males deliver an F1 generation with a shorter development time than those with permanent access, regardless of the sex of the offspring (Krueger et al., 2015).

Furthermore, the longevity and fecundity of mothers with such a limited access to males are greater compared to permanently associated females. It was assumed that the decrease in fecundity and longevity is caused by male harassment (Krueger et al., 2015). This mechanical stimulus or chemical perception of the other sex can provide reasons for the observed shift. Mechanical stimuli are known to influence fecundity and developmental rate in several insects (review: Peters & Barbosa, 1977). But chemical stimuli are also known to affect these life-history parameters in many species (Apfeld & Kenyon, 1999; Libert et al., 2007; Linford et al., 2011; Poon, Kuo, Linford, Roman, & Fletcher, 2010; Smith et al., 2008; Alcedo & Kenyon, 2004). In a study of Drosophila, the lifespan and physiology were modulated by sexual perception of the opposite sex (Gendron et al., 2014).

The aim of this study was to distinguish between the effect of mechanical male contact and olfactory contact on longevity, fecundity and developmental time of E. americanus.

## 2 MATERIALS AND METHODS

### 2.1 Rearing

A laboratory culture of E. americanus was reared under uniform conditions (23 ± 1°C, 60% humidity, light regime L:D 16:8, light on 6:00 a.m., 5,000 Lux) on potted Phaseolus vulgaris, Gossypium sp. and Hibiscus sp. plants in acrylic cages (50 × 50 × 50 cm, two sides covered with fine mesh). The culture originated from the Netherlands and has been reared in the laboratory since 2002.

To obtain virgin and naive males and females of known age, females from the laboratory culture were allowed to lay eggs in wells of 12-well Greiner plates (Sigma-Aldrich). Each well (Ø 2.2 cm) was filled with 1.5 ml of 1.4% (w/v) agar and topped with a leaf disc (Ø 1.6 cm) of P. vulgaris. Hatched larvae were separated and raised until adult eclosion and then sexed. Plates were kept in a climatic chamber under the same rearing conditions as the laboratory culture (Kumm, 2002).

To get mated individuals, freshly hatched insects were placed in couples in wells of Greiner plates (filled with agar, topped with leaf disc), kept in a climatic chamber overnight and moved to the experiment the next day. To ensure consistency in analysis of the longevity and probability of survival in mated and virgin individuals, the longevity was corrected by + 1d (virgin individuals) or rather −1d (mated individuals).

### 2.2 Bioassay

In the bioassay, individuals were reared pairwise but separated from each other by a gauze diaphragm as explained below. It allows olfactory perception but no physical contact. Longevity of the parents, fecundity of the females as well as developmental time and sex ratio of the progeny were recorded. In a second design, the known pheromonal substances (DBE5 and DBE6, Krueger et al., 2016) were added to the rearing cages and the same parameters were recorded.

Bioassay was conducted in wells (each 2 cm high, Ø 2.2 cm) of a 12-well Greiner plate (Sigma-Aldrich). They were halved by specially manufactured separators, which consisted of an acrylic frame and a circular-shaped gauze-window (Ø 1 cm, polymide, mesh size 100 µm; Franz Eckert GmbH) (Figure 1). The separator fitted perfectly into the well by height and width. Each half was filled with 2–4 mm of 1% agar.

### 2.2.1 Condition 1: Influence of presence of other individuals and mating status

In test condition 1, a semicircular-cut bean leaf (radius = 7 mm, cut with an ethanol-cleaned razor blade) was placed on the agar in each half. Freshly emerged adults (0–24 hr post-emergence) were placed into the plate wells after the scheme in Table 1 (designs 1–4) (Figure 1). The plate was covered with a glass lid and sealed with Parafilm M© (Pechinery Plastic Packaging).

Every day, adults were checked for survival. Every 2–3 days, adults were moved to new plates to provide fresh food. Hatched
laurvae were counted daily. On days 11, 13 and 15 after the females were first placed in the plate, the hatched larvae were moved individually to separate wells of a Greiner plate as described by Krueger et al. (2015) and the developmental stage of each larva was noted daily, as well as sex after emergence. On all other days, larvae obtained from mated mothers were collected in transparent plastic boxes (13 × 8 × 8 cm), which were prepared with a fresh bean leaf, pressed with its petiole and bottom into an agar-filled petri dish and a moistened cellulose paper. Boxes were kept in the climatic chamber for 12 days until emergence. The sex ratio of the adults in each box was determined. In the design with virgin mothers, the larvae were discarded after counting (except larvae collected from day 11, 13, and 15), because of the exclusive production of sons (Krueger et al., 2015; Kumm, 2002).

“Old” plates were stored in the climatic chamber for 12 days. Afterwards non-hatched proralval stages (undeveloped eggs or with failed embryonic development) were counted under a stereomicroscope.

2.2.2 | Condition 2: Influence of male pheromone substance and mating status

In test condition 2, one half of the plate well was topped with a leaf disc, the other with an equal-sized filter paper. Insects were placed according to Table 1 (designs 5–10), 40 µl known male pheromone substances DBE-5 and DBE-6 (Krueger et al., 2016) were applied on the filter paper with a pipette in a concentration of 1 mM. Distilled water (dH₂O) was used as solvent of the substances, as well as a control. The further procedure was as described above. With each change of the plate, the substance was reapplied.

2.3 | Statistical analysis

Data analysis was performed with SPSS Statistics 22 (IBM) and Winstat for Excel (Fitch Software, Bad Krozingen, Germany). Survival curves were constructed with the Kaplan–Meier method.

| Design | Half 1         | Half 2         | n   | Used shortcut in the text |
|--------|----------------|----------------|-----|---------------------------|
| (1)    | Condition 1    | female virgin  | female virgin | 64  | femaleV-femaleV          |
| (2)    | female virgin  | male virgin    | 48  | femaleV-maleV            |
| (3)    | female mated   | male mated     | 48  | femaleM-maleM            |
| (4)    | male virgin    | male virgin    | 39  | maleV-maleV              |
| (5)    | Condition 2    | female virgin  | DBE-5 | 16  | femaleV-DBE-5           |
| (6)    | female virgin  | DBE-6          | 16  | femaleV-DBE-6            |
| (7)    | female virgin  | dH₂O           | 16  | femaleV-dH₂O             |
| (8)    | female mated   | DBE-5          | 14  | femaleM-DBE-5            |
| (9)    | female mated   | DBE-6          | 16  | femaleM-DBE-6            |
| (10)   | female mated   | dH₂O           | 16  | femaleM-dH₂O             |

| TABLE 1 | Experimental design and conditions |
and compared with a log-rank test. p-values were Bonferroni corrected. Overall fecundity and developmental rate were analysed with Welch ANOVA, because of variance in homogeneity. Post hoc tests were performed with adequate Tamhane T2 (both \( p < .05 \)). Effects of the substances DBE-5 and DBE-6 on oviposition were analysed with a two-way ANOVA (with mating status and designs as co-variances, Levene test of homogeneity: \( p > .05 \)), followed by a LSD post hoc test (\( p < .05 \)). Sex ratio of progeny was analysed with chi-square goodness-of-fit tests (\( p < .05 \)).

3 | RESULTS

3.1 | Effects of pheromonal substance and individuals’ presence on parents

3.1.1 | Probability of survival of the parents

There was no effect on probability of survival of females from the presence of an additional individual or from mating status ((1) versus (2) \( \chi^2 = 0.017 \ p = .89 \); (1) versus (3) \( \chi^2 = 1.33 \ p = .25 \); (2) versus (3) \( \chi^2 = 1.24 \ p = .27 \)). Furthermore, we did not detect a difference in the males’ probability of survival ((2) versus (4) \( \chi^2 = 2.38 \ p = .12 \); (2) versus (3) \( \chi^2 = 0.004 \ p = .95 \)). Nor between males and females ((3) versus (5) \( \chi^2 = 0.44 \ p = .51 \); (2) versus (4) \( \chi^2 = 0.09 \ p = .76 \)) (Figure 2a, males not shown).

Virgin females showed no significant differences in probability of survival in the presence or absence of pheromone substances ((5) versus (6) \( \chi^2 = 1.74 \ p = .18 \); (5) versus (7) \( \chi^2 = 0.061 \ p = .8 \); (6) versus (7) \( \chi^2 = 0.65 \ p = .42 \)). Also, mated females showed no significant difference ((8) versus (9) \( \chi^2 = 0.97 \ p = .33 \); (8) versus (10) \( \chi^2 = 5.74 \ p = .016 \); (9) versus (10) \( \chi^2 = 0.96 \ p = .33 \)). But a comparison of the mating status in the presence of DBE-5, showed that the pheromone had a negative effect on the probability of survival of the mated females compared to the virgin females ((5) versus (8) \( \chi^2 = 11.36 \ p < .001 \)), whereas DBE 6 or the mating status itself (control with dH2O) resulted in no differences ((6) versus (9) \( \chi^2 = 2.97 \ p = .33 \); (7) versus (10) \( \chi^2 = 0.51 \ p = .48 \)) (Figure 2b).

3.1.2 | Fecundity and oviposition rate

There were significant differences in total fecundity (total eggs per female), oviposition rate (eggs per female/day) and hatchability in all tested designs (Welch ANOVA). Detailed data \( p \)-values are shown in Tables S1–S3.
The lowest fecundity was observed in the presence of other individuals (design (1–3)), whereas mated females produced more offspring ((3) mean = 67.87 ± 61.12 eggs/female), and virgin females produced (1) mean = 23.69 ± 23.17 eggs/female and (2) mean = 38.37 ± 33.53 eggs/female (Figure 3).

The highest fecundity occurred in virgin females treated with pheromone or dH2O. Virgin females in the presence of DBE-5 (5) produced 110.93 ± 56.04 eggs/female, virgin females in the presence of DBE-6 (6) produced 82.50 ± 60.76 eggs/female, whereas the control group (7) produced 116.07 ± 72.86 eggs/female. On the other hand, mated females treated with pheromone or dH2O, showed an intermediate fecundity rate (8) 48.64 ± 37.92 eggs/female, (9) 68.73 ± 56.82 eggs/female and (10) 95.93 ± 48.59 eggs/female (Figure 3; Table S1, S2). Two-way ANOVA showed a significant impact of mating status ($F = 7.039$, $p = .01$) on oviposition rate.

Differences between designated groups are more obvious when comparing the oviposition rates. The lowest oviposition rate was observed in virgin females associated with a virgin female ((1) 2.22 ± 2.13 eggs/female/day). The highest rate occurred in virgin (7) and mated females (10) with dH2O (7) 4.52 ± 0.78 eggs/female/day, (10) 4.87 ± 0.78 eggs/female/day). Mating status had no influence on oviposition rate (two-way ANOVA, $F = 0.511$, $p = .48$), whereas the presence of an individual did (Figure 4; Table 2, S2). Additionally,
DBE-5 had a negative effect on oviposition rate (two-way ANOVA, \(F = 4.32, p = .017\), LSD post hoc test DBE5 vs. dH20, \(p = .005\)) (Figure 4, Table S1, S3).

### 3.2 | Effects of pheromonal substance and individuals’ presence on progeny

#### 3.2.1 | Proportion of hatched prolarval stages

The proportion of hatched prolarval egg stages (hatched eggs) differed significantly only between (2) femaleV-maleV and (10) femaleM- dH2O (2) = 95.94%; (10) = 89.21%; \(p = .037\) (Table 2).

#### 3.2.2 | Development of progeny

Developmental time of progeny differed according to design (Welch ANOVA, Tamhane T2 post hoc, \(p < .05\)). Time from hatching to adult eclosion reflected the division into the three subgroups of design (1–3, 5–7, 8–10) (Figure 5). Offspring from virgin females associated with male-produced pheromones or dH2O (5–7) showed the significantly shortest developmental time. Progeny of mated mothers in the presence of pheromones or dH2O control (8–10) showed the longest developmental time, whereas offspring of mothers in the presence of another individual showed an intermediate developmental time (Table 3, S4; Figure 5). Sex of progeny had no significant effect on the developmental time (Welch ANOVA, Tamhane T2, \(p > .05\)) (data not shown).

#### 3.2.3 | Sex ratio

The sex ratio of progeny differed with the mating status of the mother (3 vs. 8 vs. 9 vs. 10) (\(\chi^2\)-goodness-of-fit-test, \(p < .05\)). The highest proportion of male progeny was produced by mated mothers associated with the mated male (3) male sex ratio 0.27, whereas mated females associated with pheromone or dH2O had a sex ratio of progeny of 0.21 (8) and 0.18 (9 and 10), respectively. All virgin mothers produced only male offspring (1/2/5/6/7) (Table 3).

### TABLE 2 Proportion of hatched prolarval stages in % of Echinothrips americanus according to design

| Design       | Sex     | n  | Proportion of hatched prolarval egg stages in % ± SD               |
|--------------|---------|----|------------------------------------------------------------------|
| (1) femaleV-femaleV | female   | 64 | 83.07 ± 28.69 a,b                                                  |
| (2) femaleV-maleV   | female   | 48 | 95.94 ± 5.89 a                                                    |
| (3) femaleM-maleM   | female   | 48 | 94.72 ± 5.73 a,b                                                  |
| (4) maleV-maleV     | male     | 39 | No offspring                                                      |
| (5) femaleV-DBE5    | female   | 16 | 93.44 ± 5.23 a,b                                                  |
| (6) femaleV-DBE6    | female   | 16 | 92.98 ± 6.49 a,b                                                  |
| (7) femaleV-dH2O    | female   | 16 | 92.69 ± 4.28 a,b                                                  |
| (8) femaleM-DBE5    | female   | 14 | 93.76 ± 5.70 a,b                                                  |
| (9) femaleM-DBE6    | female   | 16 | 91.82 ± 5.53 a,b                                                  |
| (10) femaleM-dH2O   | female   | 16 | 89.21 ± 5.74 b                                                   |

Note: Different letters indicate significant differences (Welch ANOVA, Tamhane T2 post hoc, all \(p < .05\)).
DISCUSSION

4.1 Influence on parents

The presence of a second individual without physical contact had no effect on longevity, neither on virgin nor on mated females (1–3). Mating itself did not have an effect on longevity (1/2/3), as was also found in an earlier study on *E. americanus* (Krueger et al., 2015), but not in *Franklinothrips* sp. (Hoddle, Robinson, Drescher, & Jones, 2000).

But we could find a negative effect of DBE‐5 on mated females (5) versus (8), compared to virgin ones. However, there was no significant effect of DBE 5 compared to the control (7/10), because of the Bonferroni correction. But the pheromone presence could be interpreted as a permanent presence of a male. In Krueger et al. (2015) and Li et al. (2014) permanent cohabitating with a male had a negative effect on females' longevity, which was assumed to be a result of male harassment. But in the nematode *Caenorhabditis elegans* male‐secreted substances are known to shorten lifespan (Maures et al., 2014). In *Drosophila*, female pheromones are able to modulate males’ lifespan and physiology (Gendron et al., 2014). Therefore, the often discussed negative effect of cohabitating and male harassment as a reason for shortening lifespan might be more an effect of chemical substances (Harvanek et al., 2017). In our study, the olfactory stimuli of separated males might not be enough to trigger the modulation of lifespan, which is shown under the influence of the pheromonal substances.

In this study, we did not find a significant difference in survival probability between virgin and mated males and there was no effect of whether they were male or female associated (2) versus (3) versus (4), as found for *Thrips tabaci* Lindeman males (Li, Fail, & Shelton, 2015). In a previous study, virgin males of *E. americanus* had a lower probability of survival, compared to 24h‐female‐associated males (Krueger et al., 2015). In contrast, Li et al. (2014) reported a higher probability of survival of virgin males of this species compared to mated males or female‐associated males. In our study, direct contact between individuals was prevented. The negative effect of courtship and male harassment on longevity, known from wolf spiders (Mappes, Alantalo, Kotiaho, & Parri, 1996), leaf beetles (Paukku & Kotiaho, 2005), dung beetles (Kotiaho & Simmons, 2003) and tsetse flies (Clutton‐Brock & Langley, 1997), was excluded. Presumably, a balance was formed between the negative effects shown in the previous study by Krueger et al. (2015) and the positive effects of small aggregations of individuals (known from females of *Caliothrips fasciatus* Pergande, Rugman‐Jones et al., 2012) to the similar survival probability in this study.

Virgin females held with another virgin female (1) had the lowest total fecundity and oviposition rate. Often, oviposition of virgin females in arrhenotokous species is lower than in mated ones (Li et al., 2012; Wrensch & Young, 1975). Virgin females of *Caliothrips fasciatus* stop egg laying when separated (Rugman‐Jones et al., 2012). But in contrast females held with dH 2O (7) had the highest total fecundity and also a high oviposition rate. Presumably, they recognize the

### TABLE 3

| Design | Sex ratio | Developmental time in days ± SD |
|--------|-----------|-------------------------------|
| Egg    | Larva 1   | Larva 2 | Propupa | pupa | Egg‐adult | Larva‐adult | n (development) |
| (1)    | 1.00 a    | 8.52 ± 1.10 a,b | 2.09 ± 0.78 a,b,c | 2.15 ± 0.89 a,d | 1.07 ± 0.53 a,b | 2.07 ± 0.79 a,b | 15.89 ± 1.79 a,e | 7.37 ± 1.53 a,c | 91 |
| (2)    | 1.00 a    | 7.93 ± 1.19 b | 2.03 ± 0.47 a | 2.43 ± 0.57 a,b,d | 1.09 ± 0.31 a,b | 2.22 ± 0.53 a,b | 15.71 ± 1.21 a,e | 7.77 ± 0.69 a | 134 |
| (3)    | 0.27 b    | 7.76 ± 0.89 b,c | 2.03 ± 0.49 a | 2.62 ± 0.65 b,c | 1.12 ± 0.37 a,b | 2.14 ± 0.35 a | 15.67 ± 1.02 a | 7.91 ± 0.68 b,c | 170 |
| (4)    | No offspring | | | | | | |
| (5)    | 1.00 a    | 7.92 ± 1.09 b | 1.87 ± 0.48 a,b | 2.33 ± 0.53 a,d | 1.01 ± 0.33 a | 2.23 ± 0.42 a,b | 15.36 ± 1.33 a,f | 7.42 ± 0.64 b,c | 157 |
| (6)    | 1.00 a    | 7.80 ± 1.10 b,c,d | 1.84 ± 0.46 b | 2.32 ± 0.56 a,d | 1.02 ± 0.26 a,b | 2.20 ± 0.45 a,b | 15.17 ± 1.28 b,f | 7.37 ± 0.61 b,c | 189 |
| (7)    | 1.00 a    | 7.65 ± 1.03 b,c,d | 1.84 ± 0.47 b | 2.35 ± 0.57 a,d | 1.06 ± 0.27 a,b | 2.18 ± 0.39 a,b | 15.08 ± 1.15 c,f | 7.43 ± 0.57 b,c | 145 |
| (8)    | 0.21 c    | 8.17 ± 0.96 a,d | 2.38 ± 0.65 c | 2.50 ± 0.60 a,c | 1.19 ± 0.39 b | 2.35 ± 0.56 b | 16.59 ± 1.29 d,e | 8.42 ± 0.87 d | 96 |
| (9)    | 0.18 c    | 7.92 ± 0.76 b,d | 2.14 ± 0.52 c | 2.47 ± 0.65 a | 1.18 ± 0.42 b | 2.36 ± 0.52 b | 16.08 ± 0.95 e | 8.15 ± 0.60 d | 98 |
| (10)   | 0.18 c    | 7.49 ± 0.86 c | 2.34 ± 0.65 c | 2.74 ± 0.61 c | 1.18 ± 0.47 b | 2.32 ± 0.47 b | 16.07 ± 1.21 a,e | 8.58 ± 0.89 d | 152 |

Note: Different letters indicate significant differences (sex ratio: Goodness‐of‐fit‐test, developmental stages: Welch ANOVA, Tamhane T2 post hoc, all p < .05).
presence of a second individual and adapt their egg-laying behaviour maybe by an unknown female-produced pheromone (Krueger et al., 2019). This could also be a reason for the often shown decreased oviposition rate with increased density (Kirk, 1994, 1997; Malchau, 1991).

DBE-5 had a negative effect on oviposition rate. The mating status itself has an additional impact, especially on total fecundity, whereas mated females produce fewer eggs. Virgin females held with pheromone or dH2O (5–7) tend to have a slightly higher total fecundity compared to mated females with pheromone/ dH2O (8–10). DBE-5 seems to have a slight effect more on mated females, than on virgin ones (5) versus (8).

4.2 Influence on progeny

Developmental time of the larvae is similar to previous studies (Krueger et al., 2015; Kumm, 2002), but much shorter than that found by Li et al. (2012). Nevertheless, because of the sensitivity of Thysanoptera to abiotic and biotic factors, it is difficult to compare population dynamics between different publications.

The fastest development of progeny was for individuals from virgin mothers with pheromones and control (5–7), whereas the longest development was for offspring of mated mothers (8–10). Progeny of mothers held with a second individual (1–3) had an intermediate developmental time. No difference was found between pheromonal substances and control groups (8–9 versus 10 and 5–6 versus 7). Therefore, the mating status of the mothers and the presence of an individual seem to have an influence on offspring development. This is in accordance with the former study, where progeny of permanently male-associated females had a slower development, compared to progeny of mated or virgin mothers (Krueger et al., 2015). However, male and female offspring had similar developmental times (Krueger et al., 2015). Therefore, the assumed different processes of fertilization (Li et al., 2012) or asymmetric costs for producing male or female offspring (Li et al., 2015) are not a reasonable explanation for this phenomenon.

The sex ratio of progeny differed significantly between the experimental designs. As expected, virgin females (1/2/5/6/7) produced only male offspring. This was also found by Kumm (2002), Li et al. (2012) and Krueger et al. (2015). But Oetting and Beshear (1993) (E. americanus) and Kumm and Moritz (2010) (Frankliniella occidentalis) reported a few female offspring from virgin mothers.

Offspring of mated mothers held with a mated male (3) had a higher male proportion than the mated females under pheromone or dH2O influence (8–10). E. americanus is known to alter sex ratio under certain population conditions (Krueger et al., 2015; Li et al., 2014), Haplo-diploid organisms, such as thrips, may be able to adjust their sex ratio by control of sperm access to eggs and the fertilization process (Antolin, 1993; Charnov, 1982; Clausen, 1939; Godfray, 1994; Hoddle et al., 2000; King, 1987; Kumm, 2002; Wrensch & Ebbert, 1993). The muscle insertion on the base of the spermatheca in Thripidae species (Bode, 1975) should make a controlled sperm release possible. Nevertheless, the laboratory population we used is known to be highly infected with Wolbachia (Kumm & Moritz, 2008; Chuttke et al., 2017), a well-known manipulator of reproduction and offspring sex ratio (e.g. Stouthamer, Breeuwer, & Hurst, 1999; Werren, Baldo, & Clark, 2008), but its effects are still unknown in this species.

In conclusion, female E. americanus seems to have maternal control over sex allocation and development of progeny. This supports the hypothesis of a feedback system, that is offspring in low male-biased populations develop faster and generated an adapted sex ratio (Krueger et al., 2015). However, male-biased pheromones are not able to increase the progeny male sex ratio in the same intensity as the presence of a male itself. Presumably, further mechanisms are intervening.

With regard to pheromonal substances in management strategies of E. americanus (Kirk, 2017), DBE-5 and DBE-6 are inappropriate. The slightly increased oviposition rate, fecundity in virgin mothers and the partly faster development of the progeny makes them unsuitable. But the observed decreased oviposition rate induced by other females suggests a female-produced pheromone (Krueger et al., 2019), which might be very useful in IPM strategies, and this needs to be tested further.

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CONFLICT OF INTEREST

There was no conflict of interest to one of the authors.

AUTHORS’ CONTRIBUTIONS

All authors conceived research, contributed material and read and approved the manuscript. Stephanie Krueger and Britta Müller analysed data and conducted statistical analyses. Stephanie Krueger wrote the manuscript.

DATA AVAILABILITY STATEMENT

The raw data set is available as supplementary file to this manuscript (Table S5 total analysis raw data).

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SUPPORTING INFORMATION

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