Applied Entomology and Zoology
https://doi.org/10.1007/s13355-019-00645-x

ORIGINAL RESEARCH PAPER

In vitro consumption patterns of pepper weevil, *Anthonomus eugenii* (Coleoptera: Curculionidae) on two commercial pepper cultivars in Florida

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Received: 15 February 2019 / Accepted: 4 September 2019

Abstract

The pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae), is a major pest of pepper. To analyze the consumption characteristics of pepper weevil as a reference for pest management strategies, the functional response, the intraspecific competition and the preference of *A. eugenii* were evaluated under laboratory conditions. The results showed that compared to Jalapeño, the pepper cultivar Habanero has a lower susceptibility due to the less consumption, lower searching rate and longer handling time of *A. eugenii*. Pepper weevils suffered from intraspecific competition when consuming Habanero or Jalapeño. Fruit wall thicknesses, weights and sizes were negatively correlated with the numbers of puncture marks per fruit; so, large-sized, thick-walled and large-mass fruits were less susceptible to *A. eugenii*. The present study suggests that choosing pepper cultivars and characteristics with low susceptibility to *A. eugenii*, and utilizing the intraspecific competition between pepper weevils have a potential to control the pest.

Keywords Functional response · Intraspecific competition · Preference · Habanero · Jalapeño · Pest management

Introduction

Anthonomus eugenii Cano (Coleoptera: Curculionidae), a major pest of peppers, originates from Mexico and reaches throughout Central America, southern USA and even Europe (Berdegue et al. 1994; Speranza et al. 2014). Its larvae prefer immature fruits and then cause internal fruit damage, triggering flower or fruit abscission. The life cycle of pepper weevil is about 20–30 days in the field (Genung and Ozaki 1972; Gordon and Armstrong 1990; Toba et al. 1969; Wilson 1986). Pepper weevil has three larval instars. The 1st, 2nd and 3rd instar last 1.7 d, 2.2 d and 8.4 d, respectively (Elmore et al. 1934). Its larvae are aggressive and larval cannibalism is frequently observed in intensive rearing systems (Addesso 2007). The pre-pupa and pupa stages last in about 4.9 d and 4 d, respectively. The emerging weevils escape from the fruit by creating a round hole (Capinera 2014; Goff and Wilson 1937). A female weevil can produce about six eggs a day and overall 341 eggs across its life (Patrock and Schuster 1992).

Pepper weevil infestation starts before budding and flowering (Seal and Bondari 1999); about 70–90% pepper fruits suffer from the infestation in serious areas (Rolston 1997). Since the weevil can also survive by feeding the stamens and pollen, it is difficult to control (Seal and Bondari 1999). Compared to infestation by adults, the damage from larvae is more troublesome as they cause brown and moldy cores inside fruits (Brutton et al. 1989; Webb et al. 2014), and some of which even trigger pathogens (Burke and Woodruff 1980). Pepper weevil infestation is characterized by the abscission of premature buds, flowers and fruits (Riley 1990; Seal and Schuster 1995).

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Published online: 16 September 2019

Since pesticides fail to touch the larvae inside pepper fruits, pest suppression is difficult once *A. eugenii* infestation is detected (Riley et al. 1992a, b). Therefore, the study on consumption characteristics of pepper weevils is valuable for effective IPM programs, which contributes to selecting less susceptible pepper cultivars in controlling *A. eugenii*, and utilizing the intraspecific competition between pepper weevils to suppress them, and finding specific characteristics of fruits that make pepper fruits less susceptible to pepper weevil. Choosing appropriate pepper cultivars is also important in IPM cultural control program. Since Habanero and Jalapeño have significantly fewer puncture marks than all the other commercial pepper cultivars in Florida (Seal and Martin 2016), these two pepper cultivars having relatively low susceptibilities were selected as tested cultivars. Thus in this study, we tested the consumption characteristics of pepper weevil on Habanero and Jalapeño containing functional response, intraspecific competition and consumption preference to take reasonable measures in *A. eugenii* suppression.

Materials and methods

Insect

The colony of *A. eugenii* was maintained in the Center for Biological Control, Florida Agricultural and Mechanical University, FL, USA. The weevils were reared and reproduced on the pepper plants at LD 16:8, 25 °C and 40–60% RH. All *A. eugenii* adults used in experiments were less than 12 h old, and they were starved for 24 h before the experiments. In the experiments on functional response and intraspecific competition, two commercial pepper cultivars, Habanero and Jalapeño, were selected as experimental subjects, respectively. All experiments were performed in conditions at LD 16:8, 25 °C and 40–60% RH.

Functional response

To examine the functional response of *A. eugenii* adults on pepper fruits, fruit densities tested were 20, 30, 40, 50 or 60 for a weevil adult in a plastic collapsible container (299 × 299 × 299 cm). The number of fruits consumed was examined after 24 h. Consumption by *A. eugenii* could be identified by the presence of distinctive puncture marks on the fruit. Consumption rate = damaged (or consumed) fruits/initial fruit density. Mean consumption rates among various fruit densities were calculated. Each treatment was replicated ten times simultaneously.

Intraspecific competition

To evaluate the effect of intraspecific competition on the consumption by *A. eugenii*, the fruit densities examined were 20, 40, 60, 80 and 100, for 1, 2, 3, 4 and 5 weevil adults in a plastic collapsible container, respectively. The fruit/weevil ratio was kept at 20 for each number of weevils placed together in a plastic container; the intraspecific competition for space increased with increased number of *A. eugenii* placed together. The numbers of consumed fruits at various densities were counted after 24 h, to calculate the coefficients of mutual interference. Each treatment was replicated five times simultaneously.

Consumption preference

The experiment was performed to detect the consumption preference of *A. eugenii*. A hundred pepper fruits with various sizes were collected to detect the wall thicknesses, weights and sizes. The puncture marks per fruit were counted to estimate the relationship (positive or negative) between puncture marks and fruit characteristics (wall thicknesses, weights and sizes) via linear regression analysis.

Statistical analysis

Functional response

The logistic regression analysis indicated that our data fit Holling's disc (Eq. 1) in each case; so, Holling's disc equation was used to model the relationship between the fruit consumption (N_a) and initial fruit density (N_0):

$$N_a = \frac{aTN_0}{1 + aT_hN_0}, \quad (1)$$

where N_a and N_0 are described in Eq. 1; T is the total time which in this case is 24 h, a is the searching rate; T_h is the handling time. A nonlinear regression procedure (NLR) based on the Levenberg–Marquardt method was displayed to estimate the parameters a and T_h. The starting values of a and T_h required by the NLR procedure were found by linear regressing $1/N_a$ against $1/N_0$. The resultant y-intercept is the initial estimate of T_h and the reciprocal of the regression coefficient is an estimate of a (Livdahl and Stiven 1983; Watson et al. 2000).

Intraspecific competition

The experiment was performed to calculate the coefficients of mutual interference among weevils during infestation events. Nonlinear regression analysis was performed to estimate parameters of a intraspecific competition model by fitting Eq. 2 (Hassell and Varley 1969):

$$E = QP^{-m}, \quad (2)$$

where E is the fruit consumption; P is the weevil density; m is the coefficient of mutual interference; Q is the theoretical maximum consumption rate (%). The values of Q and m were found by power-exponential regressing E and P.

Descriptive statistics were given as the mean values of ten replicates and standard errors of the mean. The mean consumption rate of *A. eugenii* between Habanero and Jalapeño was analyzed using independent-samples t test; the percentage data were arcsine $\sqrt{x}$ transformed prior to t test analysis. p values < 0.05 were considered significant. Statistics were performed with SPSS 20.0 software (IBM, Armonk, NY). Regression analyses were performed using SigmaPlot 12.0 software (Systat Software Inc., San Jose).

Results

Functional response

Pepper consumption of *A. eugenii* increased with increased densities of fruits supplied; then the consumption increased slowly and kept below a certain threshold. Thus, the functional response data for Habanero ($R^2 = 0.984$, $F_{1,3} = 247.801$, $p = 0.001$) and Jalapeño ($R^2 = 0.962$, $F_{1,3} = 101.093$, $p = 0.002$) consumption by *A. eugenii* over a 24-h period fitted the Holling's disc model well (Fig. 1). The coefficients of instantaneous searching rate (a) and handling time (T_h) indicated numerically this relationship, which had asymptotic 95% confidence intervals except 0. Pepper weevils developed less efficient skills in searching for Habanero (aT = 0.49) than Jalapeño.

(aT = 0.57). It also cost *A. eugenii* tremendous amount of time to handle Habanero (T_h = 49.09 min) compared to Jalapeño (T_h = 26.05 min). When sampling densities trended to infinity, Habanero and Jalapeño consumption thresholds were 29.33 and 55.28, respectively. Moreover, the mean Habanero consumption rate of *A. eugenii* (29.8 ± 2.1%) was significantly lower than the mean Jalapeño consumption rate (41.0 ± 2.7%) ($t = 3.269$, df = 8, $p = 0.011$). Therefore, Habanero has a relatively low susceptibility to *A. eugenii* infestation.

Intraspecific competition

When the number of pepper fruit/weevil kept 20, the mean consumption rates of weevils decreased with increased fruit–weevil density because of intraspecific competition associated with space restriction (Fig. 2). The mean Habanero consumption rate of *A. eugenii* at five fruit–weevil densities was 37.0 ± 2.6% (fruit/weevil = 20/1), 26.0 ± 2.6% (40/2), 30.3 ± 3.6% (60/3), 24.3 ± 3.4% (80/4) and 20.2 ± 2.2% (100/5), respectively. To the cultivar Jalapeño, the mean consumption rate of *A. eugenii* was 46.0 ± 2.4%, 33.0 ± 4.0%, 29.3 ± 2.4%, 31.8 ± 2.4% and 22.8 ± 1.8% at various fruit–weevil densities. The mean consumption at the different weevil densities fitted the intraspecific competition equation well; so, intraspecific competition curves based on Eq. 2 fitted the data for both Habanero ($R^2 = 0.768$, $F_{1,3} = 9.948$, $p = 0.051$) and Jalapeño ($R^2 = 0.852$, $F_{1,3} = 17.26$, $p = 0.025$). In terms of the theoretical maximum consumption rate of *A. eugenii*, Habanero (Q = 36.5%)

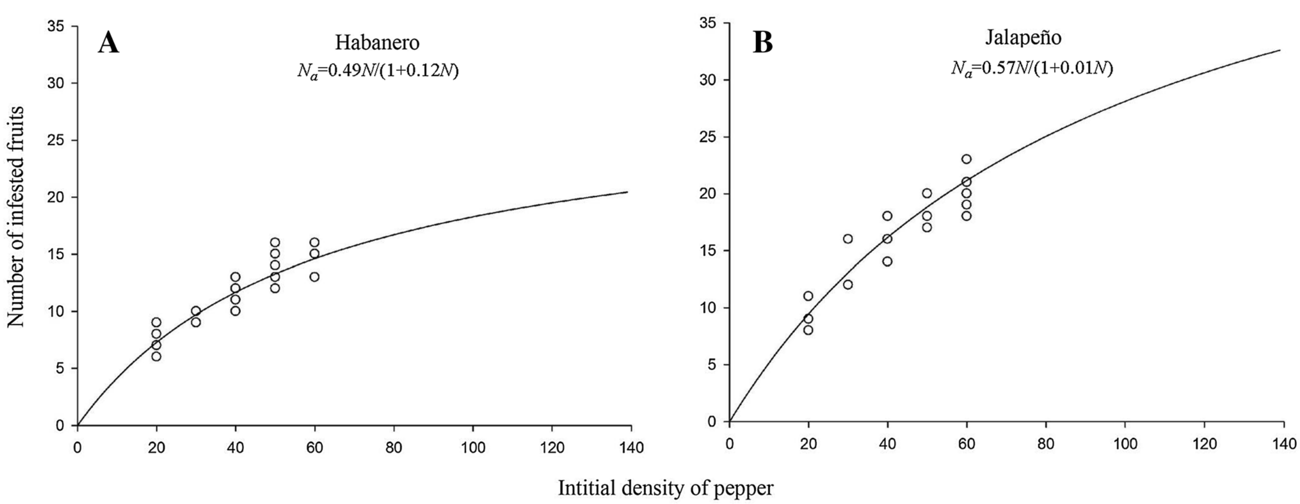

Fig. 1 Functional responses of *A. eugenii*. Solid lines showed the functional response curves of *A. eugenii* on **a** Habanero and **b** Jalapeño by fitting a Holling's disc equation (Eq. 1). Circles showed the number of fruits infested by pepper weevil

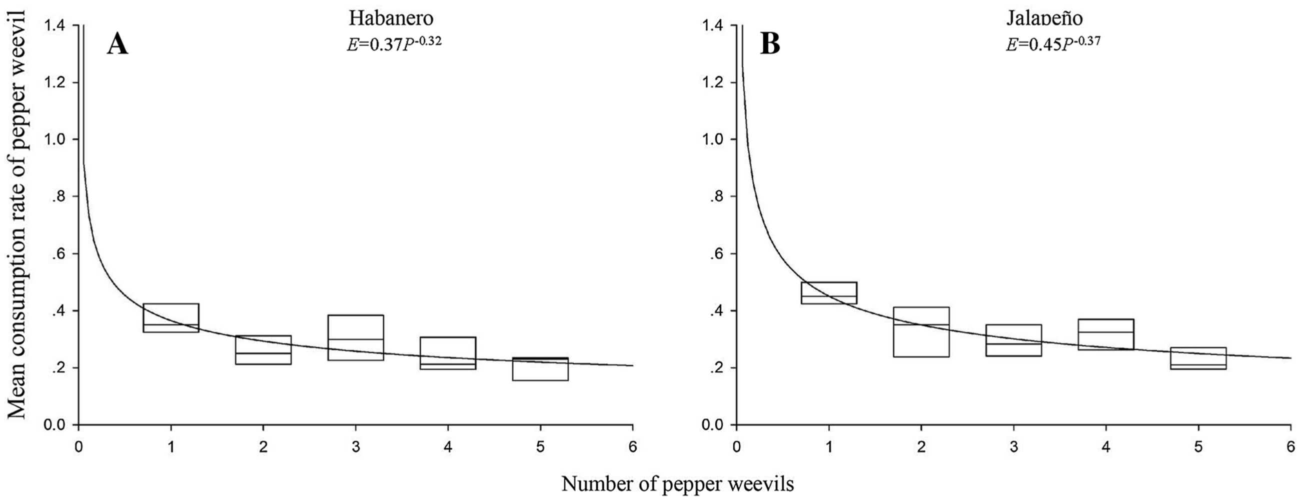

Fig. 2 Intraspecific competition among individuals of *A. eugenii* when **a** Habanero and **b** Jalapeño were consumed. Curve was fitted using the intraspecific competition equation (Eq. 2). Boxes showed the means number of *A. eugenii* with 95% confidence (largest and smallest value) as vertical bars in each plot. The ratio between number of fruit/weevil was kept 20

was lower than Jalapeño (Q = 45.1%). Pepper weevils were more greatly interfered when consuming Jalapeño (m = 0.37) rather than Habanero (m = 0.32).

Consumption preference

Fruit wall thicknesses, weights and sizes were negatively correlated with the numbers of puncture marks per fruit, and the numbers with various fruit wall thicknesses (Habanero, $R^2 = 0.568$, $F_{1,98} = 128.743$, $p < 0.001$; Jalapeño, $R^2 = 0.582$, $F_{1,98} = 136.365$, $p < 0.001$), weights (Habanero, $R^2 = 0.629$, $F_{1,98} = 166.351$, $p < 0.001$; Jalapeño, $R^2 = 0.630$, $F_{1,98} = 166.994$, $p < 0.001$) and sizes (Habanero, $R^2 = 0.656$, $F_{1,98} = 187.127$, $p < 0.001$; Jalapeño, $R^2 = 0.678$, $F_{1,98} = 206.678$, $p < 0.001$) fitted the linear equations well via linear regression analysis. Using the linear regression gets a rule of one more puncture mark on Habanero/Jalapeño for every 13.0/11.0 mm, 10.9/8.0 g or 5.5/3.4 cm^3 decrease in fruit wall thicknesses, weight or size. The average wall thickness, weight and size of a Habanero/Jalapeño fruit were $2.73 \pm 0.04/2.94 \pm 0.52$ mm, $5.20 \pm 0.06/4.52 \pm 0.77$ g and $7.98 \pm 0.11/6.98 \pm 1.74$ cm^3 (Fig. 3).

Discussion

Habanero has a relatively lower susceptibility to *A. eugenii*

Since Habanero and Jalapeño peppers attracted fewer *A. eugenii* adults (Seal and Martin 2016), both of them were selected as tested cultivars. Our study showed that the fruit consumption increased while the consumption rates diminished with increased fruit densities, and the consumption is kept below a certain threshold. This implied that *A. eugenii* showed a functional response on pepper fruits, and Holling's disc equation was the most common model analyzing the functional response (Fan and Petitt 1994, 1997).

Less consumption, lower searching rate and longer handling time of *A. eugenii* were detected in Habanero; so, Habanero was numerically preferred by *A. eugenii*, indicating Habanero may be less susceptible to *A. eugenii*. Jalapeño is a cultivar of *Capsicum annuum* which is more susceptible to *A. eugenii*; whereas Habanero is a *Capsicum chinense* cultivar that is apparently less susceptible than *C. annuum* to pepper weevils (Seal and Martin 2016). Compared to Jalapeño, Habanero may have a presumably lower susceptibility or relatively higher repellence to *A. eugenii* infestation (Seal and Bondari 1999). Thus, Habanero has the potential to produce more fruits with less insecticides; it can be served as a good selection for pepper weevil management.

Intraspecific competition caused by both physical competition and chemical communication

Our study indicated that, although the ratio of fruit to weevil numbers was kept constant at 20, the foraging efficiency gradually decreased when the weevil density became abundant in the same space due to increased space restriction per weevil. Thus, the mean consumption by *A. eugenii* was negatively impacted at high weevil densities probably due to increased chance of intraspecific competition. We found that *A. eugenii* had a higher theoretical maximum consumption rate and a coefficient of mutual interference when it infested Jalapeño rather than Habanero. Pepper weevils were digestive limited based on the results of functional response;

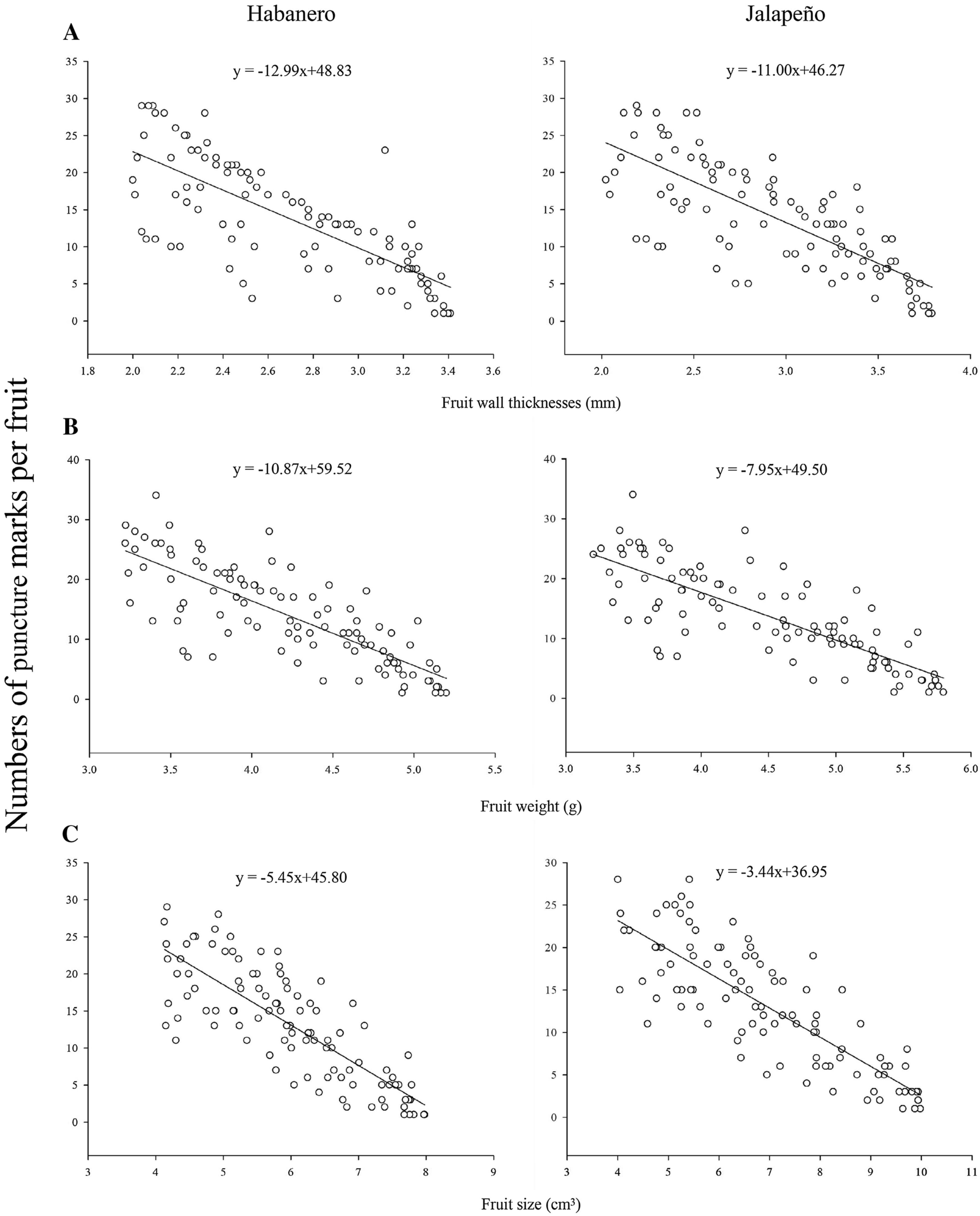

Fig. 3 Relationship between the infestation level and the fruit wall thickness (**a**), weight (**b**) or size (**c**). Each circle represents the number of puncture marks per fruit in each fruit wall thickness, weight or size. Line was fitted by linear regression analysis

so, the limitation of theoretical maximum consumption rate was tested probably because of weevil satiation. The weevils may become inactive after consuming the enough number of fruits (maximum consumption), likely minimizing mutual interference. However, when the weevils had a higher satiation level, significant time was likely to be cost on mutual interference during their foraging.

Pepper fruit damage and eggs also have some deterrent effects. During infestation, *A. eugenii* is likely to produce a host-marking pheromone excreted in the oviposition plugs and frass (Eller et al. 1994), and the potential presence of this deterrent pheromone on peppers may impact the consumption and oviposition efficient of conspecies. Producing host-marking pheromones can be detected in closely related species of *A. eugenii* (Agboka et al. 2002; Aluja and Diaz-Fleischer 2006; Anderson 2002; Stansly and Cate 1984). Moreover, fruit damage and eggs laid in the fruits may also have some deterrent effects on the selection of consumption sites (Hilker and Meiners 2006). Pepper weevils discriminate fruits infested by conspecies after assessing the cost of intraspecific competition, which impacts the decision of oviposition even consumption. Similar to the intraspecific physical competition, the intraspecific chemical communication draws increasing attention in practical application of *A. eugenii* suppression. Besides conventional insecticide and cultural control, such knowledge help to use the behavioral control method in controlling pepper weevil. It is necessary to isolate and identify the deterring pheromone from frass or oviposition plugs, and thus practically use it in IPM programs.

Large-sized, thick-walled and large-mass Habanero fruits are less susceptible

Pepper weevils preferred small-sized, thin-walled and small-mass fruits over large-sized, thick-walled and large-mass fruits. Our findings were consistent with the previous study that smaller rather than larger fruit sizes were preferred by *A. eugenii* (Toapanta et al. 2005). But unlike in our findings, some studies suggested that larger fruits may trigger more puncture marks from *A. eugenii* than small fruits due to the greater distances between sites of adult feeding; the various outcomes are possibly due to fruit size differences among the cultivars (Seal and Martin 2016). Thus, *A. eugenii* produced more feeding punctures on smaller pepper fruits than larger fruits, suggesting that well-growing peppers had a lower susceptibility to *A. eugenii*. In addition, the numerical relationship between fruit characteristics and puncture marks contributes to rapidly assessing infestation level.

Acknowledgements We thank master student Worrel Diedrick from Center for Biological Control, Florida Agricultural and Mechanical University for his assistance with this manuscript. This research was supported by Innovative Talents International Cooperation Training Project from China Scholarship Council. Partial funding support for this study from the USDA, NIFA Crop Protection and Pest Management Program is greatly appreciated.

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