Assessment of Variation in Feeding Behavior by Color Morph in the Asian citrus Psyllid (*Diaphorina citri*)

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Abstract The Asian citrus psyllid (ACP) *Diaphorina citri* (Hemiptera:Liviidae), vector of huanglongbing disease, displays a high degree of color polyphenism. In the adult stage, ACP exhibits abdominal colors that can be separated into three color groupings: blue-green, grey-brown and orange-yellow. Color morphology has been shown to influence important and energetically costly psyllid life traits including reproduction, dispersion, immune defense and resistance to insecticides. Despite this, it remains unclear how color morphology is correlated with feeding behavior. Understanding variation in feeding behavior of the ACP color morphs is critical to better understanding how ACP populations utilize host-plants and to assess potential risk for transmission of the causal agent of huanglongbing disease. We compared the feeding behavior of the three ACP color morphs by using electropenetrography (EPG). We did not detect differences in the feeding behavior activities at phloem or xylem tissues when comparing the three-color morphs. Furthermore, there were no differences in feeding behavioral parameters before

reaching phloem or xylem tissues. Our results suggest energy requirements are similar between color morphs and feeding behavior parameters associated with CLas transmission are potentially similar between color morphs.

Keywords Electropenetrography (EPG) · *Diaphorina citri* · Color polyphenism · Phenotypic plasticity · Abdominal color · Energy requirements

Introduction

The Asian citrus psyllid (ACP, *D. citri*, [Hemiptera; Liviidae]) is a sap-feeding insect pest of plants in the Rutaceae and a vector for *Candidatus Liberibacter asiaticus* (CLas), one of the main causal agents of huanglongbing (HLB) disease of citrus (Jagoueix et al. 1994; Bové 2006; Grafton-Cardwell et al. 2013). The CLas-ACP complex has devastated citrus production in several areas of the globe and remains a persistent limiting factor to the growth of the citrus industry (Singerman and Rogers 2020; Bassanezi et al. 2020). Once the vector and pathogen have established, new infestations and pathogen introductions to clean plantings are a constant threat. For successful transmission, CLas needs to be acquired when ACP ingests sap from the phloem sieve elements of an infected plant. Then, after a latency period in which the bacterium reaches the insect salivary glands, inoculation can take place when ACP salivates into the

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phloem sieve tubes of a susceptible plant. (Ammar et al., 2016; Canale et al., 2017; Bonani et al. 2010). Disrupting this sequence is one way to prevent inoculation, but this relies on a thorough understanding of the factors influencing feeding behavior (Bonani et al. 2010). Disrupting this sequence is one way to prevent inoculation, but this relies on a thorough understanding of the factors influencing feeding behavior.

Thus far, much of the research on ACP-citrus interactions has focused on characteristics of the plant host that affect ACP feeding. However, it is equally important to understand how the physiological state of the psyllid influences feeding behaviors, particularly those associated with pathogen inoculation. Psyllid species commonly show variations in body color that appear to be associated with physiological variations (Mehrnejad and Copland 2005; Soroker et al. 2013). In ACP, the abdominal color of the adult form can vary over time and changes can occur independently of abiotic factors (Wenninger and Hall 2008; Wenninger et al. 2009). The specific mechanisms underlying ACP color polyphenism are not fully understood, but nutritional status, immune response, adult maturation, and endosymbiont composition have all been implicated as playing a role (Wenninger and Hall 2008; Wenninger et al. 2009; Stockton et al. 2017; Hosseinzadeh et al. 2019). ACP color polyphenism manifests in different colors with different tones, but to facilitate categorization, previous works have described three discrete color categories each including a range of gradations between two colors as follows: grey-brown, blue-green and yellow-orange (Wenninger and Hall 2008; Wenninger et al. 2009). For blue-green morphotypes, the blue coloration is derived from pigmented cells in the fat body that contain increased levels of the copper-binding oxygen transport protein, hemocyanin (Ramsey et al. 2017; Hosseinzadeh et al. 2019). This color type is often transient; blue-green morphs may transition to the yellow-orange coloration which is associated with gravid females and adult males (Wenninger and Hall 2008). Grey-brown is the most stable coloration and is usually maintained through the entire life of the psyllid once it manifests (Wenninger and Hall 2008). Unlike the blue-green color type, underlying causes of both the grey-brown and yellow-orange color types are not known.

Even though the mechanisms behind color type shifts are not clear, ACP color morphs exhibit significant

differences in reproductive potential (Ibanez et al. 2019), reproductive behavior (Stockton et al. 2017), dispersal capacity (Martini et al. 2014), resistance to insecticides (Tiwari et al. 2013; Chen et al. 2019), cold resistance (Martini et al. 2021), immunity (Hosseinzadeh et al. 2021) and CLas acquisition and inoculation (Hosseinzadeh et al., 2019). Many of these metrics (e.g., reproduction, dispersal or immunity) are energetically demanding processes that may drive foraging and feeding behaviors required to obtain sufficient nutrients. If certain color morphs have increased energy demands, this could increase food intake (Evenden et al. 2014; Niitepöld and Boggs 2015) possibly through variation in feeding behavior.

Here, we tested the hypothesis that the three color morphs of ACP would exhibit differences in stylet activities and nutrient/water uptake while feeding on citrus hosts. To understand how color polyphenism affects ACP feeding behavior, we used electropenetrography (EPG) to compare grey-brown, blue-green and yellow-orange ACP morphs derived from a California-collected ACP population when feeding on *Citrus sinensis* cv. 'Valencia.' Since blue-green morphs perform better in activities that have higher energy demands, such as dispersal and immune response (Martini et al. 2014; Hosseinzadeh et al. 2021), we hypothesized that there would be more efficient and/or prolonged nutrient uptake bouts from phloem tissue by blue-green ACP relative to the other two color morphs. Psyllids feed from both xylem and phloem tissues, but use phloem sap as a primary source of nutrients (Hodkinson 1974; Antolinez et al. 2017; Ebert et al. 2018; George et al. 2020) linking phloem directly to the psyllid energy demands. Phloem access and exploitation is also essential for CLas transmission. Therefore, understanding how color polyphenism influences adult ACP interactions with phloem tissues will provide information about how ACP physiology affects the probability of CLas inoculation (Bonani et al. 2010; Luo et al. 2015; Wu et al. 2016; Killiny et al. 2017; Carmo-Sousa et al. 2020).

Materials and Methods

Insects

Asian citrus psyllid (ACP) adults used in this study were obtained from the insectary and quarantine facility at UC Riverside. The ACP colony was established

in 2012 from insects collected from untreated *Muraya koeniggi* plants in Azusa, California. Since establishment, the colony has been maintained, without exposure to insecticides, on Curry (*Muraya koeniggi*) and Mexican Lime (*Citrus aurantifolia*) in controlled conditions at 26–28 °C, 30–40% relative humidity (RH), and photoperiod of 14:10 (L:D). The colony was confirmed periodically to be free of *CLAs* using qPCR. All ACP used in the study were 3–13 days old adults. ACP color was identified before entering the insects into the study and sex was determined at the end of the experiment.

Plants

The feeding behavior comparison was performed in *Citrus sinensis* cv. ‘Valencia’. All plants were grown from seeds and were maintained in a greenhouse (26–28 °C, 40% RH, with natural light). The plants used in experiments were six-month-old to eight-month-old seedlings with four to six leaves. After use, plants were washed with Safer® Soap Concentrate according to the label instructions and plants were returned to the greenhouse. After the experimental run, plants were put back into the greenhouse and not reused for 30 days. In the greenhouse, the plants were fertilized once a month with MiracleGro® according to label instructions.

Probing and Feeding Behavior Comparison

Individual psyllids of each color morph were monitored when probing and feeding on citrus plants by using the electrical penetration graph technique. A minimum of 20 recordings were obtained for each color morph and a different single psyllid and plant was used for each replicate. EPG recordings were 24 h long and were performed three days a week, with two insects of each color morph per time using an eight-channel DC EPG system (Giga-8dd; EPG Systems, Wageningen, The Netherlands) with Stylet+ for Windows software (EPG Systems, Wageningen, The Netherlands). Psyllids were immobilized using a vacuum-operated plate, then, a gold wire (12 µm diameter; 2.5 cm long) was attached to the psyllid pronotum using a small drop of water-based silver glue (EPG Systems, Wageningen, The Netherlands). The opposite end of the wire was glued with the same silver glue to a brass nail. Then, the brass nail was

connected to the EPG probe and the wired insect was placed on an immature leaf (1.0 to 2.5 cm wide and 2 to 4 cm long, similar to flush described in Ebert et al., 2018) of a *Citrus sinensis* cv. ‘Valencia’ plant. A second electrode (copper, 10 cm length, 2 mm diameter) was inserted into the soil of the plant container. The psyllids were allowed to probe and feed on the abaxial surface of the leaf for 24 h. The recordings were carried out in an air-conditioned room at 26 ± 1 °C inside a Faraday cage to avoid electric field noise. EPG waveforms previously described for *D. citri* (Bonani et al. 2010) were identified as follows: NP non-probing (no stylet contact with the leaf tissue); waveform C, intercellular stylet pathway; waveform D, initial contact with phloem tissues; waveform E1, salivation into phloem sieve elements; waveform E2, phloem uptake from the sieve elements; waveform G, active intake from xylem sap.

Statistical Analysis

Data for selected EPG variables were compiled using the MS Excel Workbook for automatic EPG data compilation (Sarria et al. 2009). After compilation, all variables calculated by the Sarria’s worksheet are calculated by insect. However, the values by insect for each EPG variable were then summed and averaged. As a result, the values of the calculated EPG variables showed here maintain the names of the Sarria’s worksheet but correspond to “per insect” values (averages). Comparison between color morphs were then performed by using the SPSS 24 statistical software package (IBM Corp) with nonparametric Kruskal-Wallis test followed by pairwise comparison for variables that did not follow a Gaussian distribution and or by one-way ANOVA followed by Tuckey test for variables following a normal distribution.

Results

Color morphology did not influence the feeding behavior of variables related to xylem or phloem feeding (Table 1). The number of xylem contacts (Number of G: $H=1.48$, $df=2$, $P=0.47$) as well as the duration of xylem ingestion (Total duration of G: $H=3.21$, $df=2$, $P=0.20$) were similar among color morphs (Table 1). However, the duration of G was two times longer for blue-green morphs than for

grey-brown or yellow-orange psyllids. The number of salivation events (Number of E1: $H=1.01$, $df=2$, $P=0.60$), duration of salivation events (Total duration of E1: $H=0.51$, $df=2$, $P=0.77$), the number of ingestion events (Number of E1: $H=1.24$, $df=2$, $P=0.53$) or ingestion event duration (Total duration of E2: $F=0.11$, $df=2$, $P=0.89$) were not significantly different among color morphs (Table 1). Duration of pathway phase (Total duration of C: $F=1.15$, $df=2$, $P=0.32$), total probing time ($H=3.63$, $df=2$, $P=0.16$) and duration of non-probing ($H=3.59$, $df=2$, $P=0.16$) were also similar between color morphs. Besides, the sequential variables, time to first probe from start of the EPG ($H=0.43$, $df=2$, $P=0.80$) and time from first probe to first E1 ($H=1.14$, $df=2$, $P=0.56$) were also similar among color morphs (Table 1).

Discussion

Physiological plasticity in insects can increase survival in the face of diverse environmental challenges (Chown 2001). In ACP, color polyphenism among genetically similar individuals has been linked to physiological states that differ in important life traits such as reproductive capacity, reproductive behavior,

dispersal, resistance to insecticides, cold resistance, immunity, and interactions with microbes (e.g., CLas) (Tiwari et al. 2013; Martini et al. 2014; Stockton et al. 2017; Hosseinzadeh et al. 2019; Ibanez et al. 2019; Chen et al. 2019; Hosseinzadeh et al. 2021; Martini et al. 2021). However, associations between color morphology and feeding behavior have not been explored for all three ACP color types (blue-green, grey-brown, and yellow-orange), and investigations thus far have been limited to a single population of ACP collected in Florida (Ebert and Rogers 2020). To address this, we used EPG to study the feeding behavior of all of the three-color morph categories, which were derived from ACP collected in California. We hypothesized that previously documented variation in physiological traits between color morphs may correlate with altered feeding behavior to meet increased energy demands. However, we did not find evidence to support this hypothesis. Blue-green color morph ACP, which perform better in energy-intensive processes (Martini et al. 2014; Hosseinzadeh et al. 2021), did not differ from lower-performing color morphs in EPG parameters directly linked to phloem sap acquisition.

These results suggest that under the conditions in which most EPG experiments are performed (laboratory, with properly maintained colonies not under

Table 1 Mean and SE of probing behavior variables for blue-green, gray-brown and yellow-orange morphs of *Diaphorina citri* on *Citrus sinensis*. Different letters indicate significant differences among columns according to ANOVA or Kruskal-Wallis tests. Waveform definitions: C, intercellular stylet path-

way; G, xylem ingestion; E1, salivation into phloem sieve elements; E2 ingestion from sieve elements; and NP, non-probing. * Variables shown are sequential and conditional. *P* values shown are based on ¹One way ANOVA or ²Kruskal-wallis

Type of EPG variable	Variable name	Blue-green (n=21)	Gray-brown (n=24)	Yellow-orange (n=21)	<i>P</i> value
Non-sequential variables	Total duration of C (min)	647.76 ± 54.21 a	577.03 ± 63.31 a	507.84 ± 67.24 a	0.32 ¹
	Total duration of NP (min)	272.12 ± 51.89 a	352.18 ± 54.06 a	411.49 ± 64.12 a	0.16 ²
	Total probing time (min)	1161.50 ± 51.82 a	1080.12 ± 54.32 a	1025.42 ± 63.62 a	0.16 ²
	Number of G	3.50 ± 0.60 a	2.63 ± 0.34 a	2.52 ± 0.44 a	0.47 ²
	Total duration of G (min)	136.08 ± 42.61 a	62.63 ± 14.23 a	73.54 ± 19.59 a	0.20 ²
	Number of E1	12.35 ± 3.91 a	10.87 ± 2.52 a	12.85 ± 2.48 a	0.60 ²
	Total duration of E1 (min)	11.96 ± 3.42 a	9.59 ± 2.34 a	9.52 ± 1.56 a	0.77 ²
	Number of E2	3.95 ± 0.79 a	3.96 ± 0.57 a	5.38 ± 5.38 a	0.53 ²
	Total duration of E2 (min)	366.53 ± 70.40 a	430.83 ± 74.54 a	368.53 ± 96.52 a	0.90 ¹
	Total duration of E1 + E2 (min)	377.66 ± 72.10 a	440.84 ± 75.64 a	378.53 ± 96.88 a	0.90 ²
Sequential variables*	Time to first probe from start of EPG (min)	12.63 ± 5.77 a	12.74 ± 4.24 a	16.74 ± 7.04 a	0.80 ²
	Time from 1st probe to 1st E1 (min)	428.26 ± 88.46 a	446.40 ± 88.01a	335.37 ± 88.55 a	0.56 ²

stress) color morph polyphenism is not likely to introduce additional variation for nutrient acquisition and CLas transmission parameters. Although greater reproduction and other performance metrics for blue-green ACP color morphs should require more energy, it is possible that under ideal laboratory conditions these needs are already met. It is also possible that color morphs may differ in energy storage capacity, and that this drives differences in performance instead of behavioral parameters related to energy acquisition. Future research on color polyphenism could explore this possibility through a greater focus on ACP energy storage and metabolism.

Although we did not detect differences in phloem-related parameters among color morphs, we did detect a pattern of blue-green ACP morphs ingesting more xylem sap than the other two morphs. The xylem is nutrient poor relative to the phloem, but does provide moisture and some micronutrients (George et al. 2020). If the pattern we observed is biologically relevant, it could indicate that blue-green morphs may have different requirements for managing water balance and may try to compensate for this by modulating xylem sap intake. Additional experiments could explore this hypothesis by imposing mild osmotic stress on each color morph prior to experiments.

Although we did not explicitly test color morph influence on CLas transmission, the feeding behavior data presented here can be extrapolated to consider color morph effects based on known associations between vector feeding and the acquisition and inoculation of phloem restricted pathogens (Ebert 2019; Carmo-Souza et al. 2020). Since CLas inoculation is related to the frequency and duration of phloem salivation events (Wu et al. 2016; Carmo-Sousa et al. 2020), the lack of differences detected for the E1 parameter support the hypothesis of no correlation between color morphology and CLas inoculation. Therefore, it is likely that if there are differences in CLas transmission between color morphs, the differences could be attributed to variation in the retention or replication of the bacteria in key organs, such as the salivary glands. Field evidence and previous laboratory studies did not reveal associations between CLas titer levels and color morphology (Hall 2018; Hosseinzadeh et al. 2021). However, there could be interactive effects of CLas infection and color morph type, since CLas is known to modify ACP feeding behavior (Mann et al. 2012) and energy metabolism

(Killiny et al. 2017). Thus, although our study found minimal associations between color morph and feeding behavior in the absence of CLas infection or other stressors, future work should continue to evaluate ACP physiology in the context of color polyphenism and ecologically relevant stress conditions. Doing so will reveal the extent to which this easily observed phenotypic marker can be used to predict physiological plasticity of ACP under different management regimes.

Overall, we conclude that under the controlled laboratory conditions, the effect of color morphology in feeding behavior of non-infected ACP is negligible. This suggests color morphology will not be a likely source of noise in similar EPG experiments.

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Author's Contributions CAA, KS, MJR designed the experiments. KS, CAA conducted the experiments. CAA analyzed the data. CAA, KEM, MJR wrote the paper. MJR obtained the funding.

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Declarations

Conflict of Interest the authors declare no conflict of interest.

Code Availability Not applicable.

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References

- Ammar ED, Ramos JE, Hall DG, Dawson WO, Shatters RG Jr (2016) Acquisition, replication and inoculation of *Candidatus Liberibacter asiaticus* following various acquisition periods on huanglongbing-infected citrus by nymphs and adults of the Asian citrus psyllid. *PLoS One* 11:e0159594. <https://doi.org/10.1371/journal.pone.0159594>
- Antolinez CA, Fereres A, Moreno A (2017) Risk assessment of ‘*Candidatus Liberibacter solanacearum*’ transmission by the psyllids *Bactericera trigonica* and *B. tremblayi* from Apiaceae crops to potato. *Sci Rep* 7(45534). <https://doi.org/10.1038/srep45534>
- Backus EA, Cline AR, Ellerseick MR, Serrano MS (2007) *Lygus hesperus* (Hemiptera: Miridae) feeding on cotton: new methods and parameters for analysis of nonsequential electrical penetration graph data. *Ann Entomol Soc Am* 100:296–310
- Bassanezi RB, Lopes SA, de Miranda MP, Wulff NA, Volpe HXL, Ayres AJ (2020) Overview of citrus huanglongbing spread and management strategies in Brazil. *Trop Plant Pathol* 45:251–264
- Bonani JP, Fereres A, Garzo E, Miranda MP, Appezzato-Da-Gloria B, Lopes JRS (2010) Characterization of electrical penetration graphs of the Asian citrus psyllid, *Diaphorina citri*, in sweet orange seedlings. *Entomol Exp Appl* 134:35–49
- Bové JM (2006) Huanglongbing: a destructive, newly-emerging, century old disease of citrus. *J Plant Pathol* 88:7–37
- Canale MC, Tomaseto AF, Haddad ML, Coletta-Filho HD, Lopes JRS (2017) Latency and persistence of ‘*Candidatus Liberibacter asiaticus*’ in its psyllid vector, *Diaphorina citri* (Hemiptera: Liviidae). *Phytopathol* 107:264–272
- Carmo-Sousa M, Cortés MTB, Lopes JRS (2020) Understanding psyllid transmission of *Candidatus Liberibacter* as a basis for managing huanglongbing. *Trop Plant Pathol* 45:572–585
- Chen XD, Gill TA, Nguyen CD, Killiny N, Pelz-Stelinski KS, Stelinski LL (2019) Insecticide toxicity associated with detoxification enzymes and genes related to transcription of cuticular melanization among color morphs of Asian citrus psyllid. *Insect Sci* 26:843–852
- Chown SL (2001) Physiological variation in insects: hierarchical levels and implications. *J Insect Physiol* 47:649–660
- Ebert TA (2019) The probing behavior component of disease transmission in insect-transmitted bacterial plant pathogens. *Insects* 10:212. <https://doi.org/10.3390/insects10070212>
- Ebert TA, Backus EA, Shugart HJ, Rogers ME (2018) Behavioral plasticity in probing by *Diaphorina citri* (Hemiptera, Liviidae): ingestion from phloem versus xylem is influenced by leaf age and surface. *J Insect Behav* 31:119–137
- Ebert TA, Rogers ME (2020) Probing behavior of *Diaphorina citri* (Hemiptera: Liviidae) on Valencia orange influenced by sex, color, and size. *J Insect Sci* 20. <https://doi.org/10.1093/jisesa/ieaa016>
- Evenden ML, Whitehouse CM, Sykes J (2014) Factors influencing flight capacity of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). *Environ Entomol* 43:187–196
- George J, Kanissery R, Ammar E-D, Cabral I, Markle LT, Patt JM, Stelinski LL (2020) Feeding behavior of Asian citrus psyllid [*Diaphorina citri* (Hemiptera: Liviidae)] nymphs and adults on common weeds occurring in cultivated citrus described using electrical penetration graph recordings. *Insects* 11:48. <https://doi.org/10.3390/insects11010048>
- Grafton-Cardwell EE, Stelinski LL, Stansly PA (2013) Biology and management of Asian citrus psyllid, vector of the huanglongbing pathogens. *Annu Rev Entomol* 58:413–432
- Hall DG (2018) Incidence of “*Candidatus Liberibacter asiaticus*” in a Florida population of Asian citrus psyllid. *J Appl Entomol* 142:97–103
- Hodkinson ID (1974) The biology of the Psylloidea (Homoptera): a review. *Bull Entomol Res* 64:325–338
- Hosseinizadeh S, Higgins SA, Ramsey J, Howe K, Griggs M, Castrillo L, Heck M (2021) Proteomic polyphenism in color morphotypes of *Diaphorina citri*, insect vector of citrus greening disease. *J Proteome Res* 20:2851–2866
- Hosseinizadeh S, Ramsey J, Mann M, Bennett L, Hunter WB, Shams-Bakhsh M, Hall DG, Heck M (2019) Color morphology of *Diaphorina citri* influences interactions with its bacterial endosymbionts and ‘*Candidatus Liberibacter asiaticus*’. *PLoS One* 14:e0216599. <https://doi.org/10.1371/journal.pone.0216599>
- Ibanez F, Racine K, Hoyte A, Stelinski LL (2019) Reproductive performance among color morphs of *Diaphorina citri* Kuwayama, vector of citrus greening pathogens. *J Insect Physiol* 117:103904. <https://doi.org/10.1016/j.jinphys.2019.103904>
- Jagoueix S, Bove JM, Garnier M (1994) The phloem-limited bacterium of greening disease of citrus is a member of the alpha subdivision of the Proteobacteria. *Int J Syst Bacteriol* 44:379–386
- Killiny N, Hijaz F, Ebert TA, Rogers ME (2017) A plant bacterial pathogen manipulates its insect vector’s energy metabolism. *Appl Environ Microbiol* 83(5):e03005–e03016. <https://doi.org/10.1128/AEM.03005-16>
- Luo X, Yen AL, Powell KS, Wu F, Wang Y, Zeng L, Yang Y, Cen Y (2015) Feeding behavior of *Diaphorina citri* (Hemiptera: Liviidae) and its acquisition of ‘*Candidatus Liberibacter Asiaticus*’, on huanglongbing-infected *Citrus reticulata* leaves of several maturity stages. *Fla Entomol* 98:186–192
- Mann RS, Ali JG, Hermann SL, Tiwari S, Pelz-Stelinski KS, Alborn HT, Stelinski LL (2012) Induced release of a plant-defense volatile ‘deceptively’ attracts insect vectors to plants infected with a bacterial pathogen. *PLoS Pathog* 8:e1002610. <https://doi.org/10.1371/journal.ppat.1002610>
- Martini X, Hoyte A, Stelinski LL (2014) Abdominal color of the Asian citrus psyllid (Hemiptera: Liviidae) is associated with flight capabilities. *Ann Entomol Soc Am* 107:842–847
- Martini X, Malfa K, Stockton D, Rivera MJ (2021) Cold acclimation increases Asian citrus psyllid *Diaphorina citri* (Hemiptera: Liviidae) survival during exposure to freezing temperatures. *Insect Sci*. <https://doi.org/10.1111/1744-7917.12936>
- Mehrnejad MR, Copland MJW (2005) The seasonal forms and reproductive potential of the common pistachio psylla,

- Agonoscena pistaciae* (hem., Psylloidea). J Appl Entomol 129:342–346
- Niitepöld K, Boggs CL (2015) Effects of increased flight on the energetics and life history of the butterfly *Speyeria mormonia*. PLoS One 10:e0140104. <https://doi.org/10.1371/journal.pone.0140104>
- Ramsey JS, Chavez JD, Johnson R, Hosseinzadeh S, Mahoney JE, Mohr JP, Robison F, Zhong X, Hall DG, MacCoss M, Bruce J, Cilia M (2017) Protein interaction networks at the host–microbe interface in *Diaphorina citri*, the insect vector of the citrus greening pathogen. R Soc Open Sci 4(2):160545. <https://doi.org/10.1098/rsos.160545>
- Sarria E, Cid M, Garzo E, Fereres A (2009) Excel workbook for automatic parameter calculation of EPG data. Comput Electron Agric 67:35–42
- Singerman A, Rogers ME (2020) The economic challenges of dealing with citrus greening: the case of florida. J Integr Pest Manag 11(1):1–7
- Soroker V, Alchanatis V, Harari A, Talebaev S, Reneh S, Levsky S (2013) Phenotypic plasticity in the pear psyllid, *Cacopsylla bidens* (Šulc) (Hemiptera, Psylloidea, Psyllidae) in Israel. Isr J Entomol 43:21–31
- Stockton DG, Pescitelli LE, Martini X, Stelinski LL (2017) Female mate preference in an invasive phytopathogen vector: how learning may influence mate choice and fecundity in *Diaphorina citri*. Entomol Exp Appl 164:16–26
- Tiwari S, Killiny N, Mann RS, Wenninger EJ, Stelinski LL (2013) Abdominal color of the Asian citrus psyllid, *Diaphorina citri*, is associated with susceptibility to various insecticides. Pest Manag Sci 69:535–541
- Wenninger EJ, Hall DG (2008) Daily and seasonal patterns in abdominal color in *Diaphorina citri* (Hemiptera: Psyllidae). Ann Entomol Soc Amm 101:585–592
- Wenninger EJ, Stelinski LL, Hall DG (2009) Relationships between adult abdominal color and reproductive potential in *Diaphorina citri* (Hemiptera: Psyllidae). Ann Entomol Soc Amm 102:476–483
- Wu T, Luo X, Xu C, Wu F, Qureshi JA, Cen Y (2016) Feeding behavior of *Diaphorina citri* and its transmission of ‘*Candidatus* Liberibacter asiaticus’ to citrus. Entomol Exp Appl 161:104–111

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