# Aggregation and Feeding Preference of Gregarious *Heortia vitessoides* (Lepidoptera: Crambidae) Larvae to *Aquilaria sinensis* (Thymelaeaceae)[1]

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**Abstract** *Heortia vitessoides* Moore (Lepidoptera: Crambidae) is a pest of the evergreen tree *Aquilaria sinensis* (Loureiro) Sprenger that is endemic to China and is the source of agarwood, a valuable fragrant wood used for traditional Chinese medicinal and incense industries. *Aquilaria sinensis* is endangered due to habitat loss and other factors. Twenty-one double-choice feeding bioassays were conducted to assess the response to and preference of *H. vitessoides* larvae to leaves collected from different *A. sinensis* plants showing varying degrees of larval feeding damage in the wild. Survivorship of larvae placed in the choice arenas exceeded 85% in all but two of the choice tests. Larvae also tended to aggregate and feed on one of the leaves in the choice test rather than being evenly disbursed on the two choices. Larval aggregation and feeding on leaves collected from a tree with $<$10% foliar damage while surrounding trees exhibited >90% damage were significantly lower in all double-choice tests conducted with that tree. Furthermore, aggregation and/or feeding on leaves removed from another tree with no damage due to the natural infestation of *A. sinensis* were significantly less in all but three double-choice assays. These results indicate that aggregation and feeding behavior of the gregarious *H. vitessoides* larvae may be influenced by the source of the leaves and that there may some levels of plant resistance among the various geographic sources of the tree.

**Key Words** aggregation, *Aquilaria sinensis*, feeding preference, gregarious larvae, *Heortia vitessoides*

*Aquilaria sinensis* (Loureiro) Sprenger is an endangered tree species that produces agarwood, which is a highly prized resinous wood that is used in spices, perfumes, and traditional Chinese medicines (Liu et al. 2013). In recent years, *A. sinensis* has been cultivated in southern China to meet the increasing demands for agarwood (Liu et al. 2013). However, insects have emerged as threats to the large-scale planting of *A. sinensis*. Among these pests is *Heortia vitessoides* Moore (Lepidoptera: Crambidae), whose first through fourth larval instars are gregarious feeders with the fifth and final instar being solitary (Chen et al. 2011, Qiao et al.

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2013). *Heortia vitessoides* larvae reportedly can form large feeding groups of hundreds of larvae in a single *A. sinensis* tree, consuming all leaves within a few days (Qiao et al. 2013).

Several lepidopterans demonstrate strong larval dispersal abilities as they explore new foraging sites (Ramalho et al. 2014, Wangila et al. 2013). In gregarious species, this process can be well organized as larvae produce silk trails, release trail and aggregation pheromones, or follow tactile stimuli to initiate and maintain foraging processions (Pescador-Rubio et al. 2011, Steinbauer 2009). *Heortia vitessoides* larvae commonly form unidirectional processions on tree branches, which may extend long distances within or between *A. sinensis* trees (Qiao et al. 2013, C.W. and X.W. unpubl. data). Meanwhile, we observed that some *A. sinensis* trees growing near these infested trees showed distinctly different levels of damage, even with overlapping canopies and branches. However, the basis of these apparent preferences exhibited by *H. vitessoides* larvae on *A. sinensis* is largely unknown and led to this investigation.

In the present study, double-choice tests were conducted to compare the foraging behaviors (aggregation and feeding) of *H. vitessoides* larvae responding to leaves collected from different *A. sinensis* plants. Our study aimed to answer two questions: (a) Do *H. vitessoides* larvae make collective decisions for foraging? (b) Do *H. vitessoides* larvae have feeding preferences among different geographic sources of *A. sinensis*?

## Materials and Methods

**Insects.** *Heortia vitessoides* larvae were collected at the Tianlu Lake State Park (N 23°17′24″, S 113°21′41″) in Guangzhou, China, between 17 June and 1 July 2015. This location was designated as L1. Most *A. sinensis* trees in this location had been infested by *H. vitessoides* during the study. The infested branches were characteristically brown with light-penetrated leaves (caused by the consumption of mesophyll tissues). These branches were removed from the tree using hand-operated sheers or clippers (averruncator). Those branches with groups of *H. vitessoides* larvae present were transferred to 20-L plastic containers and transported to the laboratory within 2 to 4 h of collection. Approximately 1,000 to 1,500 larvae were collected in this manner each time. All bioassays were conducted on the same day that larvae were collected, and all larvae were used only once in the double-choice tests.

**Host plants.** In this study, a total of 24 *A. sinensis* plants were selected in two locations of the Tianlu Lake State Park, Guangzhou, China. These plants were previously introduced from different geographically based populations across southern China and showed quantitative variation in morphology (Table 1).

Three *A. sinensis* plants, designated as L1-1, L1-2, and L1-3, were selected from the L1 location where the *H. vitessoides* larvae were collected for the assays. The L1-1 plants were undamaged with no *H. vitessoides* larvae on leaves or branches when collected for bioassays conducted on 17 June 2015. However, on 3 July 2015, the L1-1 trees at that same location had >90% leaves and branches damaged by *H. vitessoides* larvae (Fig. 1A, B). On 1 July 2015, L1-2 trees growing next to the L1-1 plants (canopies overlapping) (Fig. 1A) exhibited much less

**Table 1. Leaf morphological traits (mean ± SE) of each *A. sinensis* tree used in the double-choice assays.***

| No. | Leaf Length (mm) | Leaf Width (mm) | Length:Width Ratio | Fresh Weight (mg/leaf) | Dry Weight (mg/leaf) |
|---|---|---|---|---|---|
| L1-1 | 86.5 ± 1.1 | 41.9 ± 0.6 | 2.06 ± 0.04 | 441.2 ± 15.3 | 175.4 ± 7.3 |
| L1-2 | 100.8 ± 1.7 | 46.4 ± 1.3 | 2.19 ± 0.08 | 661.3 ± 18.8 | 249.0 ± 7.2 |
| L1-3 | 80.2 ± 1.2 | 37.1 ± 0.4 | 2.16 ± 0.03 | 460.8 ± 13.1 | 189.4 ± 5.6 |
| L2-1 | 82.2 ± 1.6 | 44.7 ± 1.1 | 1.84 ± 0.04 | 471.2 ± 17.3 | 189.1 ± 6.6 |
| L2-2 | 65.4 ± 1.6 | 33.0 ± 0.8 | 1.99 ± 0.05 | 355.4 ± 14.9 | 153.1 ± 6.8 |
| L2-3 | 101.4 ± 1.1 | 43.3 ± 1.1 | 2.35 ± 0.06 | 676.6 ± 33.8 | 284.1 ± 21.2 |
| L2-4 | 75.1 ± 0.9 | 24.4 ± 0.6 | 3.09 ± 0.09 | 252.9 ± 13.0 | 116.8 ± 6.4 |
| L2-5 | 120.9 ± 3.3 | 47.5 ± 1.3 | 2.55 ± 0.06 | 717.4 ± 48.1 | 295.5 ± 21.2 |
| L2-6 | 74.7 ± 1.3 | 37.2 ± 0.7 | 2.02 ± 0.05 | 442.4 ± 19.5 | 195.8 ± 9.1 |
| L2-7 | 104.7 ± 1.9 | 46.7 ± 1.6 | 2.25 ± 0.06 | 761.5 ± 45.4 | 326.8 ± 19.6 |
| L2-8 | 87.6 ± 0.9 | 40.4 ± 1.0 | 2.18 ± 0.04 | 488.4 ± 15.5 | 209.2 ± 7.3 |
| L2-9 | 80.2 ± 1.8 | 43.5 ± 1.0 | 1.85 ± 0.05 | 459.3 ± 36.6 | 173.8 ± 16.9 |
| L2-10 | 64.3 ± 1.4 | 25.7 ± 0.9 | 2.52 ± 0.05 | 222.3 ± 13.1 | 91.4 ± 5.6 |
| L2-11 | 85.6 ± 2.2 | 36.0 ± 0.5 | 2.38 ± 0.06 | 397.1 ± 16.0 | 168.9 ± 6.9 |
| L2-12 | 85.2 ± 1.8 | 39.1 ± 1.1 | 2.19 ± 0.07 | 473.7 ± 17.8 | 186.1 ± 7.2 |
| L2-13 | 128.1 ± 3.3 | 60.7 ± 1.1 | 2.11 ± 0.03 | 946.0 ± 46.5 | 431.7 ± 17.3 |
| L2-14 | 88.0 ± 1.7 | 35.8 ± 0.5 | 2.47 ± 0.04 | 515.3 ± 23.0 | 229.3 ± 11.5 |
| L2-15 | 83.2 ± 1.0 | 30.4 ± 0.5 | 2.77 ± 0.03 | 396.8 ± 18.6 | 171.0 ± 8.8 |
| L2-16 | 93.5 ± 1.2 | 39.0 ± 1.5 | 2.42 ± 0.08 | 526.0 ± 20.8 | 213.3 ± 8.7 |
| L2-17 | 87.4 ± 2.9 | 28.7 ± 1.7 | 3.10 ± 0.13 | 332.2 ± 24.6 | 130.2 ± 10.7 |
| L2-18 | 93.4 ± 0.9 | 46.9 ± 1.1 | 2.00 ± 0.03 | 615.6 ± 20.0 | 250.9 ± 8.7 |
| L2-19 | 94.0 ± 1.9 | 39.5 ± 0.9 | 2.38 ± 0.01 | 515.9 ± 21.0 | 204.0 ± 8.1 |
| L2-20 | 94.9 ± 1.6 | 43.2 ± 1.1 | 2.20 ± 0.03 | 633.6 ± 28.4 | 236.7 ± 11.7 |
| L2-21 | 75.1 ± 1.7 | 33.2 ± 0.6 | 2.27 ± 0.05 | 344.2 ± 15.6 | 145.7 ± 7.3 |

* Ten mature leaves of each tree were randomly selected for measurement.

damage (<10% damaged) (Fig. 1B). The L1-3 trees remained undamaged throughout the study, while trees growing around the L1-3 trees showed different levels of damage (Fig. 1C). Leaves of L1-3 were collected on 25 June 2015 and 1 July 2015. Leaves from these trees (L1-1, L1-2, L1-3) were placed in double-choice assays with leaves from 21 additional *A. sinensis* trees growing in a different location in Tianlu Lake State Park. The second location (N 23°15′15″, S

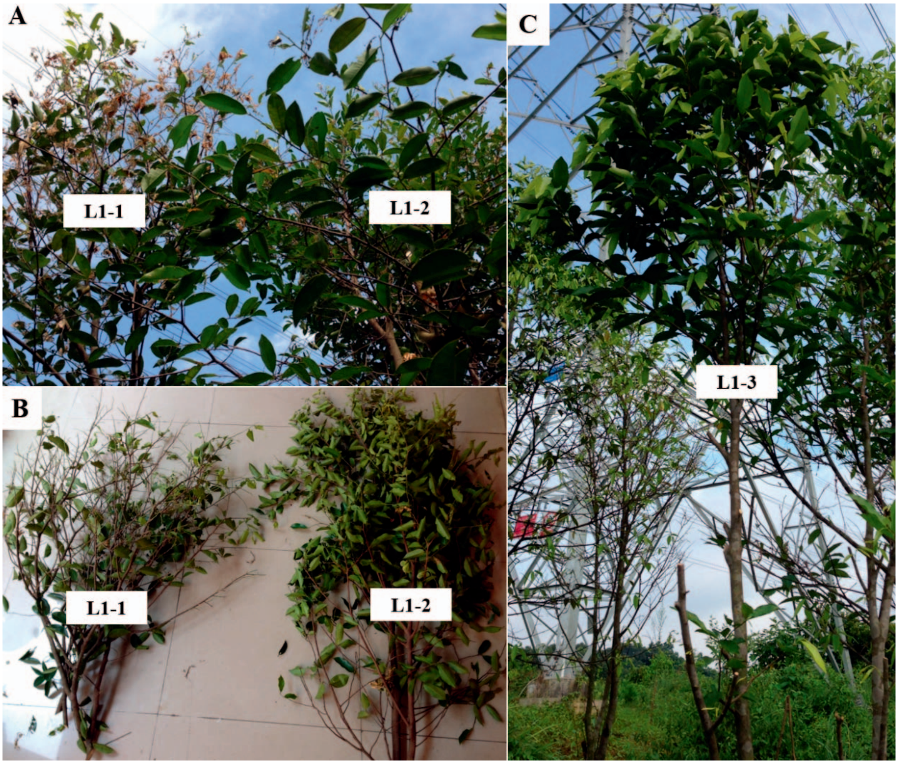

**Fig. 1. Canopies of *A. sinensis* trees at Location 1 (L1) showing L1-1 and L1-2 overlapped (A) with damage of L1-1 greater than that observed on L1-2 (B). L1-3 trees remained undamaged during the duration of the study, but surrounding trees showed higher levels of damage (C).**

113°24′51″) was designated as L2. All 21 trees at the L2 location were undamaged and not infested by *H. vitessoides* larvae as leaves were collected between 17 June and 1 July 2015.

All leaves were used in the double-choice assays within 8 h after collection. Water on the leaves was wiped with a paper towel just prior to the bioassay, and 10-cm segments of fully expanded mature leaves were placed in the bioassay arenas.

**Double-choice bioassays.** Twenty-one double-choice bioassays were conducted in this study. Leaves from the L1-1 tree (>90% damage in natural infestation) were paired with leaves collected from eight trees growing at the L2 location (trees designated as L2-1 through L2-8). Likewise, leaves from L1-2 tree (<10% damage in natural infestation) were paired with leaves cut from four trees growing at the L2 site and designated as L2-9 through L2-12. And, leaves from the L1-3 tree (no damage in natural infestation) were paired with leaves from nine trees growing at the L2 location and designated as L2-13 through L2-21. Each double-choice test was repeated six times. Bioassay arenas were transparent plastic containers (upper diameter 16 cm, bottom diameter 12.5 cm, 10 cm high). In each double-choice test, a pair of leaf segments cut from the respective trees in the comparison were placed in the opposite sides of the container and fixed with tape. Twenty *H. vitessoides* second or third instars (larval instar determined as per Qiao et al. [2013]) were transferred from infested foliage to the center of the bottom of the container using a camel-hair brush. A cover was placed over the opening of the container, and the bioassay containers were kept on a laboratory table on a 12:12-h light:dark photoperiod regime at ambient room temperature (22–26°C) for 48 h.

At that time, leaves were carefully expanded, and the area consumed by larvae was quantified using graphing paper ($1 \times 1$-mm grid). The number of larvae on each choice of leaves was counted and the total survivorship was calculated. The percentage larval concentration rate was calculated by dividing the number of larvae aggregated on and feeding on one choice of leaves by the total number of surviving larvae in the choice bioassay. This value was multiplied by 100 to yield a percentage value. In this scheme, a value of 50% indicates that larvae are evenly distributed between the two choices and, therefore, have no preference for either source. A value of 100%, on the other hand, indicates that larvae are on only one of the two choices and clearly prefer that source of leaves over the other choice.

**Statistical analysis.** Larval survivorship was compared among the 21 assays using a one-way analysis of variance (PROC GLM, SAS 9.4, SAS Institute, Cary, NC). For each individual double-choice assay, the number of larvae and leaf area consumed were compared between the two treatments using a paired *t* test (PROC TTEST, SAS 9.4). In all comparisons, significance levels were determined at $\alpha = 0.05$.

## Results

Larval survivorship did not differ significantly ($F = 0.78$; df = 20, 105; $P = 0.7348$) among the 21 double-choice assays (Table 2). Mean (± SEM) percentage survivorship ranged from 76.7 ± 8.9 to 96.7 ± 2.5. Survivorship exceeded 85% in all but two of the double-choice assays.

After release in the arenas, larvae massed together to form feeding groups and tended to aggregate and feed on one leaf in the double-choice test. Calculated larval concentration rates from the assays yielded a value >80% in most double-choice tests, with half of the tests showing a completely biased distribution (larval concentration rate value = 100%).

With only one exception, no significant differences in the number of *H. vitessoides* larvae aggregated on the respective leaves or in the area consumed by the feeding larvae occurred in choices between L1-1 leaves and each of the eight sources of leaves from the L2 site (trees L2-1 to L2-8) (Tables 3, 4). That one exception was observed with the pairing of L1-1 with L2-3, for which the area consumed was significantly lower with the L1-1 leaf (2.4 ± 1.6 $\text{cm}^2$) as compared with the L2-3 leaf (20.7 ± 6.8 $\text{cm}^2$) (Table 4). The number of larvae aggregating on L1-2 leaves was significantly lower than the numbers observed on leaves from the L2-9 through L2-12 trees (Table 3), and the amount of leaf area consumed was significantly lower on L1-2 than on the L2-9 through L2-12 leaves (Table 4). Larval numbers and/or leaf area consumed on the L1-3 entry also were significantly lower

**Table 2. Mean (± SEM) survivorship of *H. vitessoides* larvae in double-choice assays.***

| Double-Choice Test | Survivorship (%) |
|---|---|
| L1-1 vs. L2-1 | 85.8 ± 6.5 a |
| L1-1 vs. L2-2 | 76.7 ± 8.9 a |
| L1-1 vs. L2-3 | 90.8 ± 3.0 a |
| L1-1 vs. L2-4 | 87.5 ± 4.4 a |
| L1-1 vs. L2-5 | 85.8 ± 6.2 a |
| L1-1 vs. L2-6 | 96.7 ± 2.5 a |
| L1-1 vs. L2-7 | 86.7 ± 5.3 a |
| L1-1 vs. L2-8 | 81.7 ± 2.5 a |
| L1-2 vs. L2-9 | 90.0 ± 3.7 a |
| L1-2 vs. L2-10 | 90.0 ± 3.7 a |
| L1-2 vs. L2-11 | 86.7 ± 3.3 a |
| L1-2 vs. L2-12 | 90.0 ± 3.9 a |
| L1-3 vs. L2-13 | 85.0 ± 8.3 a |
| L1-3 vs. L2-14 | 85.8 ± 2.4 a |
| L1-3 vs. L2-15 | 86.7 ± 8.5 a |
| L1-3 vs. L2-16 | 91.7 ± 4.6 a |
| L1-3 vs. L2-17 | 95.0 ± 1.3 a |
| L1-3 vs. L2-18 | 92.5 ± 3.8 a |
| L1-3 vs. L2-19 | 90.0 ± 3.4 a |
| L1-3 vs. L2-20 | 88.3 ± 5.6 a |
| L1-3 vs. L2-21 | 90.0 ± 2.6 a |

* Statistical comparisons were made among all assays. Means followed by the same lowercase letter are not significantly different at $\alpha = 0.05$.

than those observed for six of nine choice comparisons in those assays (Tables 3, 4).

## Discussion

Although *A. sinensis* as a species is phenotypically and genetically diverse (Huang et al. 2014, Zhao 2007), the species has not been characterized into intraspecific taxa (i.e., subspecies, variety, forma, etc.). Based on leaf morphology, Huang et al. (2014) identified *A. sinensis* as “large-leaf” and “small-leaf” populations, but each of these groupings possess significant genetic and

**Table 3. Mean (± SEM) number of *H. vitessoides* larvae on respective *A. sinensis* leaves in each double-choice bioassay.***

| Double-Choice Test | L1- | L2- | *t* | *P*-value |
|---|---|---|---|---|
| L1-1 vs. L2-1 | 10.2 ± 2.9 a | 7.0 ± 2.9 a | 0.56 | 0.6003 |
| L1-1 vs. L2-2 | 6.3 ± 3.0 a | 9.0 ± 2.4 a | 0.52 | 0.6249 |
| L1-1 vs. L2-3 | 3.8 ± 3.3 a | 14.3 ± 2.9 a | 1.71 | 0.1489 |
| L1-1 vs. L2-4 | 5.3 ± 1.7 a | 12.2 ± 2.2 a | 1.74 | 0.1417 |
| L1-1 vs. L2-5 | 7.2 ± 3.9 a | 10.0 ± 3.4 a | 0.39 | 0.7122 |
| L1-1 vs. L2-6 | 6.7 ± 3.3 a | 12.7 ± 3.1 a | 0.94 | 0.3896 |
| L1-1 vs. L2-7 | 9.7 ± 3.2 a | 7.7 ± 3.3 a | 0.31 | 0.7683 |
| L1-1 vs. L2-8 | 10.7 ± 3.1 a | 5.7 ± 3.0 a | 0.82 | 0.4485 |
| L1-2 vs. L2-9 | 3.0 ± 1.4 a | 15.0 ± 1.4 b | 4.43 | 0.0068 |
| L1-2 vs. L2-10 | 1.8 ± 1.0 a | 16.2 ± 0.7 b | 9.30 | 0.0002 |
| L1-2 vs. L2-11 | 1.2 ± 0.6 a | 16.2 ± 0.9 b | 10.43 | 0.0001 |
| L1-2 vs. L2-12 | 2.2 ± 1.3 a | 15.8 ± 1.4 b | 5.33 | 0.0031 |
| L1-3 vs. L2-13 | 0.8 ± 0.5 a | 16.2 ± 1.6 b | 9.09 | 0.0003 |
| L1-3 vs. L2-14 | 1.0 ± 1.0 a | 16.2 ± 0.9 b | 8.04 | 0.0005 |
| L1-3 vs. L2-15 | 8.8 ± 2.6 a | 8.5 ± 2.5 a | 0.07 | 0.9468 |
| L1-3 vs. L2-16 | 9.5 ± 3.6 a | 8.8 ± 3.8 a | 0.09 | 0.9314 |
| L1-3 vs. L2-17 | 6.3 ± 2.2 a | 12.7 ± 2.2 a | 1.46 | 0.2051 |
| L1-3 vs. L2-18 | 0.9 ± 0.2 a | 17.5 ± 0.8 b | 16.64 | <0.0001 |
| L1-3 vs. L2-19 | 0.3 ± 0.3 a | 17.7 ± 0.8 b | 18.16 | <0.0001 |
| L1-3 vs. L2-20 | 0.2 ± 0.2 a | 17.5 ± 1.3 b | 12.33 | <0.0001 |
| L1-3 vs. L2-21 | 5.8 ± 3.4 a | 12.2 ± 3.4 a | 0.93 | 0.3951 |

* Means within each row followed by same lowercase letter are not significantly different at $\alpha = 0.05$ (paired *t* test).

morphological differences. In our study, leaf morphological traits (Table 1) appeared to provide little connection to the relative preference or nonpreference of *H. vitessoides* larvae on *A. sinensis*. Perhaps nutrition levels or concentrations of secondary metabolites in the leaves are involved in the observed behaviors and responses, as described in studies by Jeude and Fordyce (2014), Kumar et al. (2014), and Walker et al. (2014).

Selection of the host plant is effected by both the adult female insects in their ovipositional behavior and the offspring in their feeding preferences and survivorship (Badenes-Pérez et al. 2014a, Bernal et al. 2015, Friberg et al. 2015). Adult oviposition substrate choice reportedly is not always conducive to

**Table 4. Mean (± SEM) area ($cm^2$) of *A. sinensis* foliage consumed by *H. vitessoides* larvae in each double-choice assay.***

| Double-Choice Test | L1- | L2- | *t* | *P*-value |
|---|---|---|---|---|
| L1-1 vs. L2-1 | 8.8 ± 3.8 a | 4.8 ± 1.6 a | 0.98 | 0.3736 |
| L1-1 vs. L2-2 | 6.4 ± 2.6 a | 12.9 ± 6.8 a | 0.80 | 0.4589 |
| L1-1 vs. L2-3 | 2.4 ± 1.2 a | 20.7 ± 6.8 b | 2.74 | 0.0408 |
| L1-1 vs. L2-4 | 2.5 ± 0.5 a | 20.1 ± 7.1 a | 2.41 | 0.0610 |
| L1-1 vs. L2-5 | 13.5 ± 7.3 a | 17.5 ± 8.4 a | 0.28 | 0.7895 |
| L1-1 vs. L2-6 | 2.5 ± 0.9 a | 8.3 ± 3.7 a | 1.41 | 0.2164 |
| L1-1 vs. L2-7 | 7.8 ± 3.1 a | 3.4 ± 1.8 a | 1.00 | 0.3621 |
| L1-1 vs. L2-8 | 9.5 ± 3.2 a | 5.6 ± 2.9 a | 0.79 | 0.4639 |
| L1-2 vs. L2-9 | 5.8 ± 4.0 a | 34.0 ± 5.4 b | 3.38 | 0.0196 |
| L1-2 vs. L2-10 | 3.6 ± 1.9 a | 30.1 ± 4.2 b | 6.77 | 0.0011 |
| L1-2 vs. L2-11 | 2.2 ± 1.0 a | 32.7 ± 5.0 b | 5.25 | 0.0033 |
| L1-2 vs. L2-12 | 2.5 ± 1.7 a | 36.1 ± 5.2 b | 5.47 | 0.0028 |
| L1-3 vs. L2-13 | 1.9 ± 0.8 a | 9.2 ± 2.6 a | 2.47 | 0.0568 |
| L1-3 vs. L2-14 | 4.5 ± 1.1 a | 23.0 ± 5.1 b | 3.34 | 0.0206 |
| L1-3 vs. L2-15 | 8.1 ± 3.7 a | 12.1 ± 5.0 a | 0.52 | 0.6244 |
| L1-3 vs. L2-16 | 9.1 ± 3.8 a | 7.3 ± 3.1 a | 0.28 | 0.7888 |
| L1-3 vs. L2-17 | 8.8 ± 5.0 a | 28.6 ± 6.5 a | 1.78 | 0.1345 |
| L1-3 vs. L2-18 | 0.6 ± 0.3 a | 41.8 ± 7.2 b | 5.79 | 0.0022 |
| L1-3 vs. L2-19 | 0.4 ± 0.2 a | 24.6 ± 3.8 b | 6.41 | 0.0014 |
| L1-3 vs. L2-20 | 1.1 ± 0.7 a | 24.0 ± 2.4 b | 9.90 | 0.0002 |
| L1-3 vs. L2-21 | 3.5 ± 1.2 a | 10.5 ± 1.7 b | 5.51 | 0.0027 |

* Means within a row followed by the same lowercase letter are not significantly different at $\alpha = 0.05$ (paired *t* test).

larval feeding preference (Bernal et al. 2015, Friberg et al. 2015) and, on some occasions, is even harmful to offspring when an improper or poor-quality host was chosen as an ovipositional substrate by the adults (Badenes-Pérez et al. 2014a). In our case, we have not yet assessed ovipositional substrate choice by *H. vitessoides* because adults of this species rarely mate and oviposit under laboratory conditions (Chen et al. 2011, T.M. and X.W. unpubl. data).

The gregarious habit of first through fourth instars of *H. vitessoides* appears to serve as a basis for collective larval preferences for certain sources of *A. sinensis* trees. Our results indicate that a collective decision-making mechanism may be involved in choices or preferences of gregarious *H. vitessoides* larvae for *A.*

*sinensis* foliage. Survivorship, food consumption, growth rates, and defensive responses of gregarious lepidopteran species are often improved when compared with solitary-living counterparts (Allen 2010, Campbell and Stastny 2015). Allen (2010) reported that noncohort groups of *Euselasia chrysippe* Bates (Lepidoptera: Riodinidae) larvae assembled into groups and concluded that the benefit of living in such groups outweighs the costs of intraspecific competition of this species. Likewise, in our study, *H. vitessoides* larvae formed feeding groups even when originating from different cohorts (e.g., larvae of different cohorts were collected and mixed for the choice assays). Furthermore, we have observed that *H. vitessoides* larvae in larger groups have lower mortality rates and consume more foliage than solitary larvae (C.W. and X.W. unpubl. data).

Little to no chemical pesticide residue is one of the basic requirements for the production of high-quality agarwood, especially when it is used for medicinal and food-additive purposes. Therefore, it is important to reduce the use of chemical pesticides for *H. vitessoides* control. Naturally occurring levels of resistance among different sources of *A. sinensis* trees to its pest *H. vitessoides* that were observed in this study may serve as initial impetus for studies on the responses observed. A "push–pull" strategy might be suggested, using nonpreferred *A. sinensis* trees to repel (push) *H. vitessoides* larvae while the preferred plants attract (pull) larvae. The preferred plants can be treated with chemical pesticides (Badenes-Perez et al. 2014b, Shelton and Nault 2004) and, therefore, become "dead-end traps" for *H. vitessoides* larvae. Larger-scale screenings of *A. sinensis* trees for preference or nonpreference by *H. vitessoides* larvae should be explored further.

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