Variation of Body Size in Rice Water Weevil (Coleoptera: Curculionidae) and Its Associations with Population Biology

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Abstract

Life history characteristics help us to determine the ability of invasive species to establish and thrive in an exotic environment. However, so far, there have been very few reports concerning geographic variation in the body size of invasive insects and the associations between body size variation and population biology. In this study, we surveyed the geographic variation in body size of an invasive agricultural pest, the rice water weevil Lissorhoptrus oryzophilus Kuschel (Coleoptera: Curculionidae), in China. Its body size variation was found to follow Bergmann’s rule, a size cline related to latitude/altitude in which weevils tended to be larger in higher latitude/altitude localities. Moreover, using adults of different body size within populations, we also characterized the relationship between body size and some population traits of this weevil, including reproduction, food consumption, cold tolerance, and agility. The results showed that, large and mid-size adults (within populations) tended to consume more rice leaves, and larger adults also laid more and longer eggs, when compared with smaller adults. However, smaller adults appeared to have higher agility. In conclusion, body size of rice water weevil varies significantly with geography, and body size variation (within populations) may affect life history traits.

Key words: phenotypic plasticity, body size, adaptation, reproduction

Life history characteristics are among the major factors affecting the invasiveness of alien insects (Hemptinne et al. 2012, Seiter and Kingsolver 2013). For example, insects that have high reproductive potential and strong resistance to environmental stresses are more likely to establish in a new geographic range (Wan and Yang 2016). Thus, determining associations of life history traits with invasiveness is crucial for risk analysis and management of non-native species.

Body size can affect insects’ performance and adaptation. For example, for a given insect species, large females may enjoy more reproductive advantages than small females, such as higher fecundity and mating capacity (Honěk 1993, Blay and Yuval 1999, Durocher-Granger et al. 2011). Larger individuals may also have greater movement ability (Yang 2000). In particular, larger individuals are potentially more tolerant to cold because they may have a larger fat reserve (Ellers et al. 1998, Colin et al. 2007), slower heat loss owing to a smaller surface-to-volume ratio (Smith et al. 2000, Merrick and Smith 2004), or a higher warming-up rate (Stone 1993), which support them to have a higher survival rate during overwin-tering (Kovacs and Goodisman 2012, Baranovska and Knapp 2014). However, despite the overwhelming evidence for benefits, being larger is costly and insects generally do not evolve toward larger sizes (Blanckenhorn 2000, Gotthard et al. 2007). In contrast, under conditions of limited resources or environmental stresses, small body size can be more beneficial, allowing insects to become harder against starvation (Couvillon and Dornhaus 2010, Blanckenhorn 2011), be more resistant to high temperatures (Carroll and Quiring 1993), have more investment to immunity (Busso et al. 2017), and be more favored in male mating competition (Blanckenhorn et al. 1995, Yasuda and Dixon 2002).

Body size of insects can increase with latitude (elevation), displaying a Bergmann’s rule (BR), or decrease with latitude, displaying a converse Bergmann rule (CBR), both of which are common in nature (Blanckenhorn and Demont 2004, Pincheira-Donoso 2010, Shelomi 2012). BR and CBR clines are presumably caused by temperature and season length, respectively (Blanckenhorn and Demont 2004). Besides, other factors such as genetic variation, voltinism, humidity, food supply and natural enemies can also influence the body size clines across latitudes (Chown and Klok 2003, Scharf et al. 2009, Horne et al. 2017).

However, despite the knowledge described above, only a few studies have focused on body size in invasive insects, which include the carabid beetle Merizodus soledadinus (Guerin-Ménéville)
(Coleoptera: Carabidae) (Laparie et al. 2010, 2013), the leafminer fly *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) (Tantowijoyo and Hoffmann 2011), the big-headed ant *Pheidole megacephala* (Fabricius) (Hymenoptera: Formicidae) (Wills et al. 2014), and the cabbage white butterfly *Pieris rapae* (L.) (Lepidoptera: Pieridae) (Seiter and Kingsolver 2013). Moreover, so far, very few reports have examined geographic variation in the body size of invasive insects, and little is known about the associations of body size with their performance and adaptation. Knowledge of this field is important for evaluating the invasiveness of alien species and their adaptive ability to new environments.

The rice water weevil *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae) is one of the most important pests of rice in east Asia (Chen et al. 2005, Wan and Yang 2016). Adults feed on rice leaves leaving typical longitudinal scars and larvae consume roots, ultimately leading to yield loss (Stout et al. 2002). This weevil is native to North America, and since the late 1950s has expanded into the northwestern United States (California) and Asian countries like Japan, North Korea, South Korea, and China (Saito et al. 2005). It reproduces parthenogenetically in all of non-native regions, and thus, all of the adults are females (Huang et al. 2017). In China, this weevil was first detected in 1988 (Tanghai, Hebei Province) and has since spread to 24 provinces. It is univoltine in northern China where single-cropping rice is grown; newly emerged adults first feed in rice fields or adjacent habitats and then move to overwintering sites before rice is harvested. However, it is bivoltine in the southern regions growing double-cropping rice, where the second generation generally has a low density due to the formation of diapause in the majority of first-generation adults (Zhu et al. 2005, Huang et al. 2017). So far, little is known about body size variation in this weevil.

In this study, we first surveyed several morphological traits of rice water weevil adults in different geographic populations, with the aim of determining whether body size varies with geography. After detecting significant geographic variation in body size, we assessed the possible biological significance of this variation. To do this, we compared adults of different body sizes within populations, as within-population variation in insect body size is a relatively common response to changed environmental conditions (e.g., temperature and food quality), and this type of body size variation can also have major effects on insects’ performance (Navarro-Campos et al. 2011, Garrad et al. 2016). We, thus, assess characteristics of within-population adults to provide a basis for the analysis of body size variation at the geographic level.

### Materials and Methods

**Adult Collection and Morphometric Measurements**

Rice water weevil adults (all female) were collected from six locations in China during April–June in 2014 and 2015. Locations are >750 km apart; Yuanping and Xundian have an elevation of >800 m, while the others have an elevation below 100 m (Table 1, Fig. 1). These locations represent the major rice growing regions or the regions heavily invaded by rice water weevil in China. The weevil has spread to more northern and southern regions beyond this range, but these populations were not used in our study because of the difficulty of finding them in recent years due to effective control or relatively low natural density.

Within 48 h after collection, 100 adults were randomly sampled from each population, and 4 morphometric traits were measured for each adult: length of the pronotum (Prnt-L), length of the elytra (Elt-L), width of the elytra (Elt-W), and distance from the fore-pronotum to the end of the elytra (Brd-L) (Fig. 2). Of them, elytral length has been frequently used for studies of coleopteran body size (e.g., Schmitz et al. 2000, Smith et al. 2000, Hernandez et al. 2011, Knapp and Uhmann 2014). The other three have also been shown to be relevant with body size (Cook 1993, Smith et al. 2000, Fowler et al. 2015). As we did not know which trait(s) would be most reasonable for rice water weevil, we first measured each of them and then screened for the best one using principal component analysis (see Statistical Analysis). The measurements were performed under a stereo microscope (Nikon SMZ-645, Japan) equipped with an ocular micrometer. Each individual was gripped at the body with forceps, fixed on the object stage, and then measured. The morphometric data were averaged within populations, and the association of body size with geography was analyzed as described in the statistical analysis section.

### Comparisons of the Supercooling Points of *L. oryzophilus* Adults of Different Body Sizes

The supercooling point (SCP), termed as the temperature at which body water begins to crystallize when exposed to freezing temperatures, is often used as an indicator of insect cold-hardiness (Sinclair et al. 2015). Overwintering *L. oryzophilus* adults were collected from Xiangxiang and Tongcheng from 19 December to 23 December 2014, when the adults were in diapause but had not experienced the local lowest winter temperatures, which generally occur during January. For each population, adults were measured using the method described above, and then sorted into three groups: large, mid-size, and small adults, which accounted for ca. 15, 70, and 15% of total adults, respectively. These percentages fit for the fact that large and smaller individuals were much fewer than moderately-sized individuals. Next, 18–22 adults were randomly sampled from each group, and the SCP of each adult was measured using a 4-pathway supercooling-point determination system (Senyi, Jiangsu Economic Development Co., Ltd., Nanjing, China) according to the manufacturer’s instructions. During the measurements, the weevil abdomen was fixed to the tip of a semiconductor thermal probe with sellotape and then wrapped in absorbent cotton. The SCP was compared among the three groups within population.

### Comparisons of Leaf Consumption, Reproduction, and Survival of *L. oryzophilus* Adults of Different Body Sizes

Two groups of adult collected during second time for all weevils of overwintered adults, which were collected from Xiangxiang and

### Table 1. Information about the geographic locations where rice water weevils were collected and evaluated

| County, province | Latitude, longitude; elevation | Year the weevil was first found | Collection date |
|------------------|--------------------------------|-------------------------------|-----------------|
| Tanghai, Hebei   | 39°17’N, 118°28’E; 5 m         | 1988                          | 12 June 2014; 25 April 2015 |
| Yuanping, Shanxi | 38°42’N, 112°46’E; 824 m        | 2003                          | 27 May 2014; 18 May 2015   |
| Tongcheng, Anhui | 31°12’N, 117°01’E; 48 m         | 2001                          | 26 May 2014; 29 April 2015 |
| Yueqing, Zhejiang| 28°03’N, 120°59’E; 7 m          | 1993                          | 15 May 2014             |
| Xiangxiang, Huan | 27°48’N, 112°38’E; 68 m          | 2005                          | 5 May 2014; 24 April 2015 |
| Xundian, Yunnan  | 25°32’N, 103°20’E; 1871 m        | 2007                          | 11 May 2014             |
Yuanping during late April of 2016 and early May of 2016, respectively, were used separately in this experiment. For each population, adults were first sorted into large, mid-size, and small groups as described above, and then 15–18 adults were randomly sampled from each group to observe their feeding, oviposition, and survival, with each adult serving as a single replicate. The adults were reared individually in glass tubes (2.5 cm diameter, 24 cm length) containing tap water to a depth of 5 cm and one 20-d-old rice plant (cultivar Nei 5 You 8015, Zhejiang Nongke Seed Co., Ltd., Hangzhou, China). The tubes were kept in chambers at 26 ± 1°C and 60–70% humidity with a photoperiod of 16:8 (L:D) h. The plants were replaced every 4 d; the lengths of adult feeding scars on the plants were measured and the eggs in the leaf sheaths were counted. Moreover, at least 10 eggs were randomly sampled for each adult around the middle ovipositional stage, and their lengths were measured under a stereo microscope (Nikon SMZ-645, Japan) with an ocular micrometer. Egg hatching success was also observed as described previously (Chen et al. 2012), using eggs deposited on three different dates for each body-size group, with nine replicates each consisting of 28–50 eggs deposited by at least 10 females. When observations ended, total leaf consumption (cumulative length of feeding scars), total number of eggs deposited, ovipositional period, adult survival duration, egg length and hatching percentage were determined and subsequently compared among body size groups.

Comparisons of the Agility of L. oryzophilus Adults of Different Body Sizes

Six groups of overwintered adults were collected from Xiangxiang, Tongcheng, and Yuanping from late March to early July of 2015 and were used separately in this experiment (Fig. 3). The adults were first sorted into large, mid-size, and small groups and then agility assays were performed for the large and small groups. We took the flip time of adults as an indicator of their agility (see Jiang et al. 2007).

Adult individuals oriented ventral-side up were allowed to fall freely from a height of 5 cm to the center of a flat filter paper (9.0 cm diameter; Wohua Filter Paper Co., Ltd., Hangzhou, China). The weevils flipped to right their position; the time required by the weevils to flip (hereafter ‘flip time’) was recorded with a stop watch. This procedure was repeated twice in succession for each weevil. At least 20 weevils were measured for each body-size group. If a weevil failed to right itself within 5 min, testing of the individual was terminated and its flip time was excluded from the analysis. For each successful weevil, the two measured flip times were averaged and the mean was used for data analysis. To reduce error, large and small adults were measured alternately. Flip time was compared between the large and small adults within each population.

Statistical Analysis

All data analyses were performed using the statistical software system SPSS v.20 (IBM SPSS Statistics, 2011). Because morphometric variables may be correlated to each other, principal component analysis (PCA) was first performed to replace the four original variables (Prnt-L, Elt-L, Elt-W, and Bd-L) with new variables, i.e., principal components. Then, the first principal components (PC1s) of each population were used as dependent variables, and one-way analysis of variance (ANOVA) was performed to test the significance of body size variation with geography, at the significance level (P) 0.05. Such an analysis was performed separately for the data of 2014 and 2015. Moreover, for each population, t-tests were performed to compare body size between the 2 yr.
One-way ANOVA was used to analyze the relationships between body size and adult SCP, leaf consumption, egg production, ovipositional period, survival duration, egg length and hatching percentage. Prior to ANOVA, data were tested for homogeneity of variance (Levene test), and the following transformations were made previously: the leaf consumption data were square-root transformed, egg numbers were square-root transformed (x + 1), and egg hatching percentages were arcsine square-root transformed. Means were compared by performing Tukey’s honest significant difference (HSD) post hoc tests at P = 0.05.

Data of flip time was first tested for homogeneity of variance, and then compared between large and small adults by performing t-tests at P = 0.05.

Results
Geographic Variation of L. oryzophilus Adult Body Size
Values of each measured morphometric traits were given in Table 2. PCA showed that the PC1s explained 82.9% (in 2014) and 87.9% (in 2015) of the total variance and were correlated positively with all four morphometric variables (Supp Table 1 [online only]). Therefore, PC1s were retained for comparison among populations. Besides, Bd-L (length of pronotum + elytra) exhibited the highest correlation with PC1s (Supp Table 1 [online only]), thus it was chosen as a representative indicator of body size for the analyses below.

ANOVA showed that body size varied significantly with geography in both years (2014: F = 10.361; df = 5, 594; P < 0.001, 2015: F = 20.412; df = 3, 396; P < 0.001). In 2014, body size in the Yuanping (northern) population was similar to those in the Tonghai (northern) and Xundian (southern but with high elevation, Table 1) populations but significantly larger than in the other three (southern) populations. In 2015, body size in the Yuanping population was significantly larger than in the other three populations. In contrast, in both years, the Tongcheng and Xiangxiang (southern) populations were significantly smaller in body size than the Yuanping and Tonghai (northern) populations. For each population, no significant difference was found in body size between the 2 yr (Tanghai: t = 0.801; df = 191.700; P = 0.424, Yuanping: t = –1.062; df = 198; P = 0.290, Tongcheng: t = –0.936; df = 198; P = 0.351, and Xiangxiang: t = 0.982; df = 198; P = 0.328; Table 3).

Comparisons of the SCPs of L. oryzophilus Adults of Different Body Sizes
We measured the SCPs of adults with different body sizes collected from Xiangxiang and Tongcheng. Within each population, the SCPs of adults did not vary significantly with body size (Xiangxiang: F = 0.528; df = 2, 58; P = 0.592, and Tongcheng: F = 1.073; df = 2, 55; P = 0.349), and differently sized adults had similar SCPs (Table 4).

Comparisons of Leaf Consumption, Reproduction, and Survival of L. oryzophilus Adults of Different Body Sizes
Large and mid-size adults consumed more rice leaf tissue than small adults, and the difference was statistically significant in the Xiangxiang population. The number of eggs deposited was significantly related to body size in both Xiangxiang and Tonghai populations (Table 5). Large and mid-size Xiangxiang adults deposited 65.1 and 49.3% more eggs, respectively, than small adults, while large and mid-size Tonghai adults deposited 100 and 40.0% more eggs. Egg length was significantly related to adult body size, and the eggs produced by large and mid-size adults tended to be longer than those produced by small adults. None of the other traits, including ovipositional period, adult survival duration, and egg hatching percentage, differed significantly across adult body sizes (Table 5).

Discussion
The ability of invasive insects to colonize and spread in new geographic ranges is related to morphological, physiological, or behavioral traits (Piiroinen et al. 2011, Laparie et al. 2013). We found that the adult body size of rice water weevil, an invasive insect pest in east Asia, varied significantly with geography. Adults of northern (Tanghai and Yuanping) populations and a population at high elevation (Xundian) tended to be larger than those from southern populations (Tongcheng and Xiangxiang), exhibiting a body size pattern of Bergmann’s rule.

It is not clear what ecological factors cause the geographical variation in L. oryzophilus adult body size. According to Bergmann’s rule (Blankenhorst and Demont 2004), temperature can be speculated as a major cause. Other factors may also play a role, such as the quality of host plant the larvae feed on, as this will vary with rice variety or/and phenology.

Within populations, large L. oryzophilus adults did not have significantly lower SCPs than small adults, and there was no consistent

| Year | Geographic population | No. of adults | Prnt-L (mm) | Elt-L (mm) | Elt-W (mm) | Bd-L (mm) |
|------|-----------------------|---------------|-------------|------------|------------|-----------|
| 2014 | Tanghai               | 100           | 0.724 ± 0.002 | 2.302 ± 0.005 | 1.438 ± 0.004 | 3.031 ± 0.006 |
|      | Yuanping              | 100           | 0.731 ± 0.002 | 2.322 ± 0.007 | 1.455 ± 0.005 | 3.055 ± 0.008 |
|      | Tongcheng             | 100           | 0.715 ± 0.004 | 2.260 ± 0.009 | 1.385 ± 0.007 | 2.977 ± 0.011 |
|      | Yueqing               | 100           | 0.715 ± 0.003 | 2.297 ± 0.010 | 1.397 ± 0.006 | 3.011 ± 0.013 |
|      | Xiangxiang            | 100           | 0.711 ± 0.003 | 2.279 ± 0.010 | 1.395 ± 0.006 | 2.989 ± 0.012 |
|      | Xundian               | 100           | 0.712 ± 0.002 | 2.333 ± 0.009 | 1.432 ± 0.006 | 3.044 ± 0.011 |
| 2015 | Tanghai               | 100           | 0.745 ± 0.003 | 2.359 ± 0.007 | 1.410 ± 0.005 | 3.042 ± 0.009 |
|      | Yuanping              | 100           | 0.759 ± 0.003 | 2.382 ± 0.008 | 1.453 ± 0.004 | 3.075 ± 0.008 |
|      | Tongcheng             | 100           | 0.741 ± 0.003 | 2.317 ± 0.007 | 1.393 ± 0.006 | 2.994 ± 0.010 |
|      | Xiangxiang            | 100           | 0.735 ± 0.003 | 2.343 ± 0.008 | 1.383 ± 0.006 | 2.990 ± 0.011 |
have as high fecundity as expected. Another factor is, because the size and accordingly larger weevils (at higher latitudes) may not for reproduction. This might potentially reduce the overall reproduction. However, it is not clear whether such associations also existed among geographic populations. That is, an association also exists among geographic populations. Therefore, the body size and fecundity associations, and the advantages of large size should be much more complicated than expected and need further research in the future.

Body size can affect insect activities, such as foraging (Greenleaf et al. 2007, Guédor et al. 2009), moving (Marden and Kramer 1995, Yang 2000, Samejima and Tsubaki 2010, García and Sarmiento 2012, Cooper et al. 2013), competition (Moya-Laraño et al. 2007), and avoiding attack by natural enemies (Remmel and Tammaru 2009). By increasing body, thorax and/or wing size, insects may increase mobility, which, in turn, affects their adaptability to diverse environments (Saastamoinen 2007, Laparie 2013). We found that larger L. oryzophilus adults had longer and wider elytra (Table 2). However, it is unclear whether such adults would have higher flight capacity and have advantages in flight-supported activities over adults with small elytra.

In our flip-time observations, small adults were found to be more agile (righting their body position more rapidly) than large adults. This agility might have advantages, such as allowing small adults to more easily escape from attacks of natural enemies. This provides valuable empirical evidence for the benefits of small size in insects, which has intrigued the interest of some researchers (Blankenhorn 2000, Chown and Gaston 2010).

Table 3. PC1 values (mean ± SE) for rice water weevils from six populations

| Populations | PC1 in 2014 | PC1 in 2015 |
|-------------|-------------|-------------|
| Xiangxiang  | 0.19 ± 0.07abA | 0.10 ± 0.08bA |
| Mid-size    | 0.43 ± 0.08A  | 0.55 ± 0.09A  |
| Small       | -0.43 ± 0.11dA | -0.29 ± 0.10cA |
| Yueqing     | -0.09 ± 0.11bcd | -  |
| Xiangxiang  | -0.23 ± 0.09cA  | -0.37 ± 0.11cA |
| Xundian     | 0.13 ± 0.10abc | -  |

Means within a column followed by the same lowercase letter are not significantly different (P > 0.05, Tukey’s test). Means within a row followed by the same capital letter are not significantly different (P > 0.05, t test)

Table 4. SCPs (mean ± SE, °C) of L. oryzophilus adults of different body sizes

| Populations | Adult group | Bd-L (mm) | SCP (°C) |
|-------------|-------------|-----------|----------|
| Xiangxiang  | Large       | 3.092 ± 0.007(22)a | -14.2 ± 1.1(22)a |
|             | Mid-size    | 2.908 ± 0.005(20)b | -14.4 ± 1.1(20)a |
|             | Small       | 2.614 ± 0.023(19)c | -15.7 ± 1.1(19)a |
| Tongcheng   | Large       | 3.168 ± 0.006(18)a | -18.1 ± 0.6(18)a |
|             | Mid-size    | 3.010 ± 0.004(20)b | -16.0 ± 1.1(20)a |
|             | Small       | 2.807 ± 0.024(20)c | -17.0 ± 1.1(20)a |

Means within a column followed by the same letter are not significantly different (P > 0.05, Tukey’s HSD test). Numbers in parentheses are the numbers of adults observed.

Table 5. SCP values (mean ± SE) for rice water weevils from six populations

| Populations | SCP (°C) |
|-------------|----------|
| Xiangxiang  | -14.3 ± 0.6°C |
| Mid-size    | -14.4 ± 1.1(20)°C |
| Small       | -15.7 ± 1.1(19)°C |
| Yueqing     | -  |
| Xiangxiang  | -0.23 ± 0.09cA  |
| Xundian     | 0.13 ± 0.10abc |

In summary, L. oryzophilus has successfully invaded a large geographic area in China and exhibits geographic variation in adult body size, which increases with altitude. Moreover, by studying within-population adults of different body size, we showed that body size is relevant with this weevil’s population biology: larger weevils consume more leaf area, lay more and larger eggs, but are less agile than small weevils. Yet, due to the limit of our observations, we do not know whether such associations also existed among various geographic populations. To be noted, geographic variation in body size and associated life history traits reflect different life history strategies appropriate to and shaped by the environmental conditions present in different geographic locations. Certainly, results obtained from within-population studies cannot be used to infer the biological significance of body size variation among geographic populations. Despite this, our study is valuable describing for the first time associations between body size and biological traits in rice water weevil. In the future, transplantation experiments are to be performed, that is, putting weevils originating from one population to the environmental conditions experienced by other populations and then measuring the biology traits. Moreover, such experiments will also allow us to learn whether the variation of body size in this weevil is the result of phenotypic plasticity or is the result of genetic variation among populations (local adaptation). In addition, as voltinism may affect patterns of insect body size (Blankenhorn and Demont 2004, Horne et al. 2017), we need to learn whether this weevil’s body size, as well as possible consequences of body size and size variation, will change in southern China. There it originally had two annual generations, but in future, this will shift because rice is increasingly grown in a single season which can only support one weevil generation per year (Zhu et al. 2005, Huang et al. 2017).

There aspects will be studied in the future, once a viable of method artificially rearing these weevils has been developed. Although rearing has been attempted, the specificity of larvae and pupae’s oxygen-intake system has so far proved difficult to simulate consistently in the laboratory (Zhang et al. 2006).
Table 5. Feeding, reproduction and survival traits (mean ± SE) of adults with different body sizes

| Populations | Adult group/size | Avg. no. of ovipositional eggs deposited | Egg length (mm) | Egg hatch percentage | Adult survival duration (days) | ANOVA value | P value |
|-------------|------------------|----------------------------------------|-----------------|----------------------|-------------------------------|-------------|---------|
| Xiangxiang Large | 3.152 ± 0.007(18)a | 26.4 ± 1.9(17)a | 0.95 ± 0.00(17)b | 9.9 ± 0.00(17)a | 81.1 ± 1.9(36)a | 0.89 ± 0.00(17)a | 87.7 ± 1.9(36)a |
| Xiangxiang Mid-size | 2.900 ± 0.007(18)b | 154.7 ± 8.8(17)a | 0.99 ± 0.00(17)b | 9.9 ± 0.00(17)a | 91.0 ± 1.9(36)a | 0.95 ± 0.00(17)a | 91.0 ± 1.9(36)a |
| Xiangxiang Small | 2.663 ± 0.020(18)c | 118.2 ± 6.2(17)b | 1.01 ± 0.00(17)c | 9.9 ± 0.00(17)a | 91.0 ± 1.9(36)a | 1.03 ± 0.00(17)c | 91.0 ± 1.9(36)a |
| Xiangxiang | 2.900 ± 0.007(18) | 154.7 ± 8.8(17) | 0.99 ± 0.00(17) | 9.9 ± 0.00(17) | 91.0 ± 1.9(36) | 0.95 ± 0.00(17) | 91.0 ± 1.9(36) |
| Tanghai Large | 3.178 ± 0.005(15)a | 21.6 ± 1.1(11) | 0.95 ± 0.01(15)a | 9.9 ± 0.01(15)a | 91.0 ± 1.9(36) | 0.95 ± 0.01(15)a | 91.0 ± 1.9(36) |
| Tanghai Mid-size | 3.178 ± 0.005(15)b | 85.7 ± 13.8(11)a | 0.95 ± 0.01(15)b | 9.9 ± 0.01(15)a | 91.0 ± 1.9(36)a | 0.95 ± 0.01(15)b | 91.0 ± 1.9(36)a |
| Tanghai Small | 2.873 ± 0.010(15)c | 42.9 ± 5.1(11)b | 0.95 ± 0.01(15)c | 9.9 ± 0.01(15)a | 91.0 ± 1.9(36)a | 0.95 ± 0.01(15)c | 91.0 ± 1.9(36)a |
| Tanghai | 3.178 ± 0.005(15) | 85.7 ± 13.8(11) | 0.95 ± 0.01(15) | 9.9 ± 0.01(15) | 91.0 ± 1.9(36) | 0.95 ± 0.01(15) | 91.0 ± 1.9(36) |

Numbers in parentheses are the numbers of adults or eggs observed. Leaf consumption and egg number data were square-root transformed and hatching percentage data were arcsine square-root transformed to meet normality assumptions. Means ± SE within a column followed by the same letter are not significantly different (p > 0.05).

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