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Oviposition Preference and Offspring Performance of Mechoris ursulus (Coleoptera: Attelabidae) in Cyclobalanopsis glaucoides (Fagales: Fagaceae) and Quercus franchetii (Fagales: Fagaceae) in Central Yunnan, China

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Source: Journal of Insect Science, 15(1) : 1-5

Published By: Entomological Society of America

URL: https://doi.org/10.1093/jisesa/iev005

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RESEARCH

Oviposition Preference and Offspring Performance of *Mechoris ursulus* (Coleoptera: Attelabidae) in *Cyclobalanopsis glaucoides* (Fagales: Fagaceae) and *Quercus franchetii* (Fagales: Fagaceae) in Central Yunnan, China

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Subject Editor: Evan Preisser

J. Insect Sci. 15(19): 2015; DOI: 10.1093/jisesa/iev005

ABSTRACT. *Mechoris ursulus* (Roelofs) (Coleoptera: Attelabidae) is a pest weevil of Fagaceae oak trees in eastern Asia. The female has a distinct branch-cutting behavior in conjunction with oviposition in the acorns of its host plant. This study analyzed the factors influencing oviposition preference by carrying out continuous field surveys over the course of 2009–2010 and through laboratory rearing. The field survey showed that for both of the hosts, *Cyclobalanopsis glaucoides* Schottky (Fagales: Fagaceae) and *Quercus franchetii* Skan, *M. ursulus* preferred branches with fewer acorns and larger acorns on the same branch for oviposition. Laboratory rearing experiments showed offspring performance (i.e., survival rate and fresh weight of larvae) was significantly and positively correlated with acorn size. Preference for larger acorns could maximize the fitness of offspring by providing sufficient food source and space.

Key Words: ovipositing preference, reproductive behavior, oak nut weevil, size of acorn, number of acorn

Oviposition preferences have a profound effect on offspring growth, survival, and population persistence (Stiling 1988, Cornell and Hawkins 1995). Although a number of factors may influence oviposition preference, larval nutrition is especially important since it directly influences larval growth and development (Sogawa 1982; Mikenberg and Ottenheim 1990; Nakamura et al. 1995a,b; Abutsu and Togashi 2000; Hu et al. 2009).

The oak nut weevil, *Mechoris ursulus* (Roelofs) (Coleoptera: Attelabidae), is a univoltine, phytophagous, economically important beetle that is found throughout eastern Asia, which feeds on many trees in the family Fagaceae (Koo et al. 2003, Xiao et al. 2007). In China, this weevil has recently been listed as a dangerous forest pest by the State Forestry Administration of China (SFA 2013). Female *M. ursulus* lay eggs in acorns from August to October and follow this by cutting the branch used for oviposition (Choi et al. 1993, Koo et al. 2003). Although most of the branches with oviposited acorns are completely cut off from the hosts, a small number remain connected by the periderm (as observed in this study). The branch-cutting behavior of female adults and the fruit-boring behavior of larvae are a major factor in the limited natural regeneration of many Fagaceae populations (You et al. 2001, Yu et al. 2001).

Available studies on the bionomics of *M. ursulus* are limited (You et al. 2001), and research on its oviposition preferences are scarcer still. Koo et al. (2003) reported the oviposition preference and offspring performance on *Quercus serreta* (Thunberg) and *Q. mongolica* (von Fischer ex Ledebour) under laboratory conditions. The insufficient knowledge on the oviposition preference and the concealed immature stage have become the bottleneck in the integrated pest management of *M. ursulus*.

Increasing *M. ursulus* infestation of Fagaceae in Yunnan Province (southwestern China) threatens the vast forests of this region. The Fagaceae found on the Central Yunnan altiplano are ecologically important, as they are one of the principal components of the local semihumid evergreen broadleaf forests (Wu et al. 1987, Shen et al. 2005). The climate and vegetation of this region differ substantially from other localities with *M. ursulus* where previous research has been conducted. The Central Yunnan altiplano has less severe but drier winters, a higher average altitude, and a unique assemblage of Fagaceae species (Chen 2001, Shen et al. 2005, Xiao et al. 2007). Although these abiotic differences may affect *M. ursulus* oviposition behavior and offspring performance, the performance of *M. ursulus* under these distinct natural conditions have not been investigated.

Our goal was to study the oviposition behavior of *M. ursulus* under natural conditions in central Yunnan and to analyze the factors which influence oviposition preference and offspring performance. Understanding these factors will assist in the formulation of effective management strategies for this species.

Materials and Methods

Field Sites and Plant Species. Two field sites with semihumid evergreen broadleaf forests were selected near Kunming, central Yunnan. One site was the Fagaceae garden of the Kunming Institute of Botany, Chinese Academy of Sciences (KIB; 25° 01′ N, 102° 41′ E, 1,980 m, Kunming, China). The major species at the site are *Cyclobalanopsis glaucoides*, *Quercus franchetii*, *Q. variabilis*, and *Q. aliena*. The other site was situated in the Stone Forest Scenery Spot (SF; 24° 49′ N, 103° 19′ E, 1,780 m, Kunming, China). The major Fagaceae species there are *C. glaucoides* and *Q. franchetii*.

C. glaucoides Schottky (Fagales: Fagaceae) and *Q. franchetii* Skan make up 25.2% of the semihumid evergreen broadleaf forests in central Yunnan (Shen et al. 2005). Preliminary investigation of the *M. ursulus* infestation confirmed that *C. glaucoides* and *Q. franchetii* were the most damaged species among all the Fagaceae tree species distributed in central Yunnan (observed in this study).

Field Survey. To assess branch-level acorn density of uncut branches on both *C. glaucoides* and *Q. franchetii*, 5–10 individuals of each host

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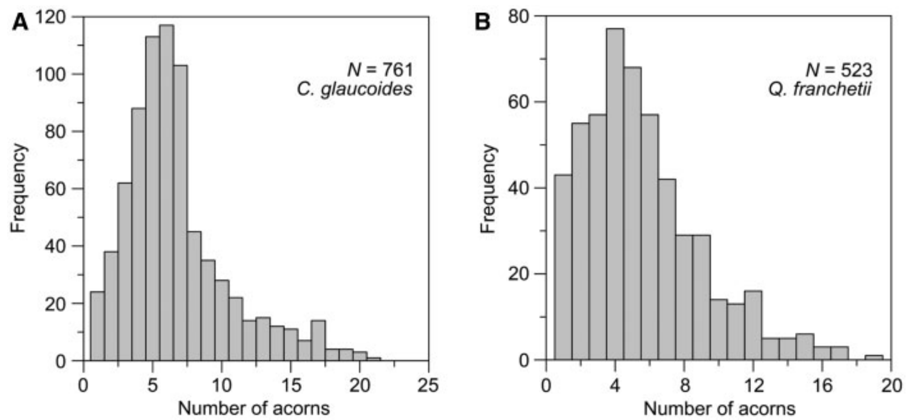

Fig. 1. The overall frequency distribution of the number of acorns on the branches of *C. glaucoides* (A) and *Q. franchetii* (B) surveyed in 2010 under natural condition, with *N* indicates the number of acorns.

Table 1. Model summary of linear regression analysis between the number of acorns and branch diameter

Host[a]	Variable	SE	*B*	β	*t*	*P*
CG	Constant	0.007	0.218	—	32.074	<0.001
	No. of acorns	0.002	0.008	0.272	3.883	<0.001
QF	Constant	0.004	0.214	—	60.629	<0.001
	No. of acorns	0.001	0.004	0.213	4.677	<0.001

[a]Host species: CG, *C. glaucoides*; QF, *Q. franchetii*.

species with *M. ursulus* infestation were selected from the field sites in 2010. For each individual tree, the number of acorns on branches growing at different cardinal positions on the tree was counted.

Sample Collection. Samples (branches cut by *M. ursulus*) were collected from August to September in both 2009 and 2010. All samples of *Q. franchetii* were collected from the KIB site, whereas samples of *C. glaucoides* were collected from the KIB site in 2009 and from the SF site in 2010. The grounds of sampling sites were cleaned thoroughly prior to collection. Newly cut branches were collected daily around 1700 hours. Acorns of the collected branches were carefully examined to separate acorns which had experienced oviposition from undamaged acorns, by the oviposition puncture and plug in the cupules.

Oviposition Preference and Offspring Performance. Although existing research indicates that acorn size is the most important factor influencing *M. ursulus* oviposition preference (Koo et al. 2003), this does not mean that other factors like branch diameter are unimportant: branch cutting is an energy-consuming activity, and the female may also choose thinner branches. Based on this, this study first needed to evaluate the magnitude of correlation between branch diameter and the number of acorns. Therefore, for both *C. glaucoides* and *Q. franchetii*, the diameter of each cut branch was measured to 0.01 mm with a 0–200 mm Vernier caliper (Shanghai, China), and the number of acorns on the branch was counted. The acorns of cut branches were then measured with the same Vernier caliper and size was calculated as cm^3.

The oviposited acorns were divided into two sets. For the first set, 600 acorns were sorted into three groups containing 200 pieces of each of large, medium, and small-sized acorns (the mean volume of acorns in each size class is presented in Table 3). Acorns of three categories were separately sealed into three nylon bags (40 by 80 cm, 80 holes per inch) and placed on the ground of the KIB site. The mature larvae exiting from the acorns were collected daily and weighed on a Sartorius BP110S electronic scale (Sartorius AG, Germany). For the second set, a total of 190 acorns of *C. glaucoides* and 261 acorns of *Q. franchetii* were measured to 0.01 mm using Vernier calipers and then placed in test tubes (3 cm in diameter, 10 cm in length) lined with damp sand. These were then incubated at 25°C in an SPX-250B-G climate controlled growth chamber (Shanghai Boxun Industry Co., Ltd., Shanghai, China) for 40 d. The larvae were extracted from the acorns after incubation, and these acorns were sorted into two groups based on how much of endosperm had been consumed (partially eaten and completely eaten). The numbers of living and deceased larvae were used to calculate the survival rate, and the living ones were weighed on the same electronic scale. As some larvae died from various causes during the course of rearing, the acorns with partially eaten endosperm were not analyzed here.

Data Analysis. Data were used to calculate the frequency distribution of acorn numbers on cut and uncut branches, the ratio of oviposited acorns compared with the total number of acorns, the mean size (cm^3) of both oviposited and nonexploited acorns, and the mean fresh weight (g) and survival rate of larvae reared from large, medium, and small-sized acorns.

To analyze whether the diameter of branches differs with the change of number of acorns, a linear regression was also applied to determine the magnitude of correlation between the branch diameter and the number of acorns. Analysis of variance (ANOVA) was used to compare the size of oviposited and nonoviposited acorns on cut branches from both *C. glaucoides* and *Q. franchetii*. Linear regression was used to assess the relationship between acorn size and fresh larval weight for completely eaten acorns. ANOVA was used to compare the fresh weight of larvae reared from small, medium, and large acorns. SPSS 13.0 (SPSS Inc., Chicago, IL) was used for all calculations and analyses.

Results

Number of Acorns Under Natural Conditions. The 2010 field survey showed that uncut branches of *M. ursulus*-infested *C. glaucoides* had 1–21 acorns ($N_{\text{branch: 2009}} = 189$; $N_{\text{branch: 2010}} = 118$; $N_{\text{acorn}} = 761$). Branches with ≤ 3 acorns comprised 16.3% of surveyed branches, branches with 4–7 acorns comprised 55.3%, and branches with ≥ 8 acorns comprised 28.4% (Fig. 1A). Uncut branches from *M. ursulus*-infested *Q. franchetii* had 1–19 acorns per branch ($N_{\text{branch: 2009}} = 231$; $N_{\text{branch: 2010}} = 197$; $N_{\text{acorn}} = 523$). Branches with ≤ 2 acorns comprised 18.7% of surveyed branches, branches with 3–7 acorns comprised 57.6%, and branches with ≥ 8 acorns comprised 23.6% (Fig. 1B).

Branch Diameter, Number of Acorns, and Acorn Size. A total of 307 ($N_{\text{branch: 2009}} = 189$; $N_{\text{branch: 2010}} = 118$) *C. glaucoides* branches and 428 ($N_{\text{branch: 2009}} = 231$; $N_{\text{branch: 2010}} = 197$) *Q. franchetii* branches were collected. The number of samples used in each specific analysis will be shown in corresponding charts and tables.

For *C. glaucoides*, the linear regression analysis between the number of acorns and the branch diameter did not show strong positive correlation ($R = 0.272$, adjusted $R^2 = 0.069$), and for *Q. franchetii*, the linear regression analysis between the number of acorns and the branch diameter did not show strong positive correlation ($R = 0.213$, adjusted $R^2 = 0.043$) (Table 1). The ANOVA analysis showed significant

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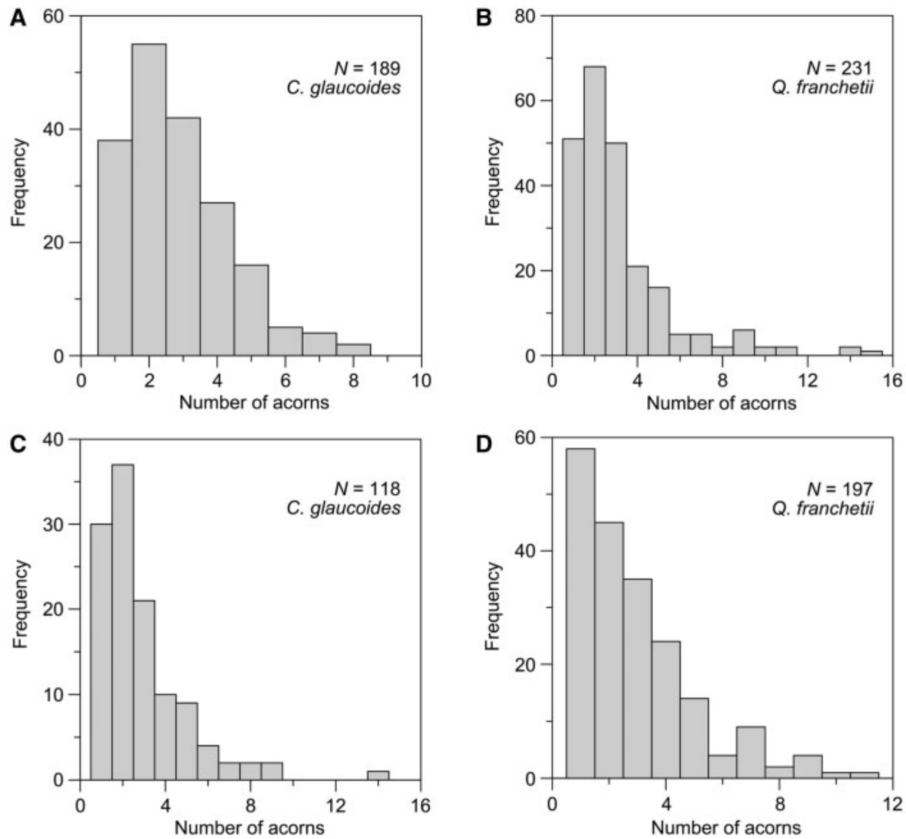

Fig. 2. Frequency distribution of the number of acorns on the oviposited (cut) branches of *C. glaucoides* (A and C) and *Q. franchetii* (B and D) collected in 2009 (A and B) and 2010 (C and D), with *N* indicates the number of branches.

Table 2. Comparison of mean acorn sizes and the ANOVA analysis of the nonexploited acorns and the oviposited acorns

Year	Host[a]	Type[b]	Acorn size (cm^3)	No. of acorns	Mean square	*F*	*P*
2009	CG	NE	1.041 ± 0.624	105	11.505	31.081	<0.001
		OV	1.511 ± 0.592	429			
	QF	NE	0.872 ± 0.492	212	7.005	27.004	<0.001
		OV	1.128 ± 0.526	509			
2010	CG	NE	1.003 ± 0.276	71	7.232	28.937	<0.001
		OV	1.400 ± 0.651	26			
	QF	NE	0.807 ± 0.270	93	8.113	65.878	<0.001
		OV	1.116 ± 0.416	34			

[a]Host species: CG, *C. glaucoides*; QF, *Q. franchetii*.
[b]Acorn type: OV, oviposited; NE, nonexploited.

difference of acorn size among branches with different number of acorns (1–4 vs. ≥ 5) ($N_{acorn} = 352$, $F = 2.734$, $P < 0.01$) for *C. glaucoides*; it also showed significant difference of acorn size among branches with different number of acorns (1–3 vs. ≥ 4) ($N_{acorn} = 368$, $F = 2.865$, $P < 0.01$) for *Q. franchetii*.

Influence of Acorn Numbers. The statistical results for the collected samples showed that the number of acorns of *C. glaucoides* on the oviposited branches cut by *M. ursulus* ranged from 1 to 8 (2009: $N_{branch} = 189$) and 1 to 14 (2010: $N_{branch} = 118$), a range from 1 to 4 being common, comprising 85.7% and 83.8% of the total number of cut branches and branches with 2 acorns being the most common (29.1% and 31.6%, respectively). Branches with ≥5 acorns only comprised 14.3% and 16.2% of the total number of the cut branches sampled from the 2 yr (Fig. 2A and C). For *Q. franchetii*, the number of acorns on the cut branches ranged from 1 to 15 (2009: $N_{branch} = 231$) and 1 to 11 (2010: $N_{branch} = 231$), with a range from 1 to 3 being common, comprising 73.2% and 82.2% of the total number of the cut branches and branches with two acorns and one acorn being the most common (29.4% and 29.4%, respectively). Branches with ≥5 acorns only comprised 10.8% and 17.8% of the total number of the cut branches sampled from the 2 yr (Fig. 2B and D).

Influence of Acorn Size on Oviposition and Offspring Performance. On both *C. glaucoides* and *Q. franchetii,* acorns chosen by *M. ursulus* for oviposition were significantly larger than the nonexploited ones (Table 2), and the weight of larvae reared from large acorns was significantly greater than that of larvae reared from small acorns (Table 3). Larval survival was also positively correlated with acorn size (Table 3).

Most of the living larvae excavated from the acorns reached the final instar after 40 d of incubation in the second set of rearing experiments. Larval survival ratio in *C. glaucoides* acorns was 60.0% ($N_{acorn} = 190$); larval survival ratio in *Q. franchetii* acorns was 54.8% ($N_{acorn} = 261$). There was a significant positive correlation between acorn size and larval weight when the endosperm of the acorns was completely eaten (*C. glaucoides*: $R = 0.810$, $N_{acorn} = 88$, adjusted $R^2 = 0.652$, $P < 0.001$; *Q. franchetii*: $R = 0.829$, $N_{acorn} = 117$, adjusted $R^2 = 0.685$, $P < 0.001$) (Fig. 3).

Discussion

Our study first analyzed the statistical difference of branch diameter among branches with different number of acorns and then evaluated the magnitude of correlation between branch diameter and the number of acorns. Although both of the ANOVA and the linear regression produced statistical results with significance, the correlation between the above-mentioned two variables was rather weak, as determined by the low *R* and adjusted R^2 values of the linear regression for both host species. Hence, the authors believed that branch diameter was not the major factor which influenced the oviposition preference of *M. ursulus*.

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Table 3. Influence of acorn size relative to offspring performance of *M. ursulus* and the ANOVA analysis for statistical difference among larval weight

Host[a]	Type	Acorn size (cm^3)	Fresh weight of larvae (g)	Survival rate of larvae (%)	Mean square	F	P
CG	Large	2.932 ± 0.324	0.0679 ± 0.0985	66.5	0.025	5.809	0.004
	Medium	1.307 ± 0.214	0.0349 ± 0.0563	56.0			
	Small	0.237 ± 0.193	0.0270 ± 0.0096	26.5			
QF	Large	1.879 ± 0.130	0.0402 ± 0.0111	65.0	0.005	41.804	< 0.001
	Medium	0.970 ± 0.104	0.0373 ± 0.0111	54.0			
	Small	0.116 ± 0.132	0.0248 ± 0.0087	33.5			

[a]Host species: CG, *C. glaucoides*; QF, *Q. franchetii*.

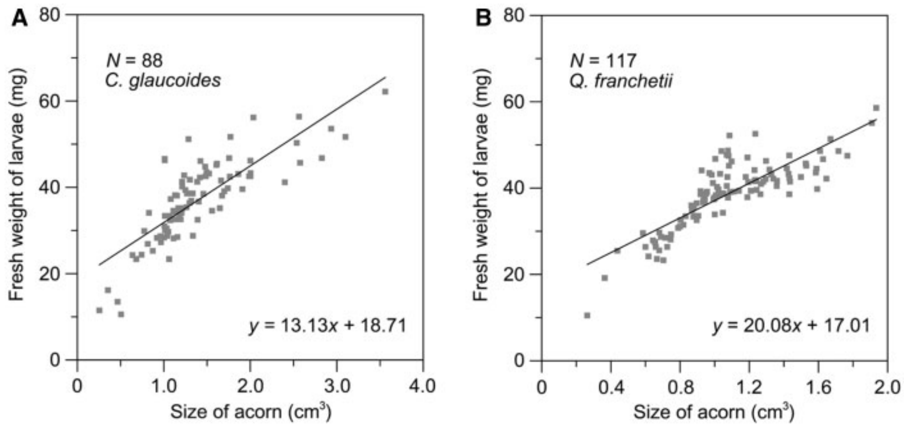

Fig. 3. Relationship between acorn size and weight of larvae reared from completely consumed acorns of *C. glaucoides* (A) and *Q. franchetii* (B).

Our study showed that *M. ursulus* preferred branches with fewer acorns for oviposition by comparing the frequency distribution of the number of acorns between oviposited branches and the surveyed branches. Our analysis also showed that the size of acorns on branches with fewer acorns was significantly larger than those on branches with more acorns. Oviposited acorns were also significantly larger than nonexploited acorns (Table 2). Koo et al. (2003) speculated that female *M. ursulus* assess acorn size by walking around acorns between oviposition events. Our results and this previous research both suggest that *M. ursulus* selects larger acorns for oviposition.

The rearing experiment demonstrated that larvae living in large acorns weighed more and survived better than larvae living in small acorns (Table 3). In cases where the acorn endosperm was completely consumed, larval weight was significantly and positively correlated with acorn size (Fig. 3). This finding supports the results of oviposition preference of *M. ursulus* reported by Koo et al. (2003). The preference of *M. ursulus* for larger acorns is consistent with the "preference-performance theory" proposed by Thompson (1988) and Gripenberg et al. (2010), that the parental oviposition behavior and preference should maximize the survival and development potential of the offspring in phytophagous insect.

A previously unseen behavior of *M. ursulus* was observed during the course of field work. Prior to oviposition, emerged female adults fed on both the leaves and tender acorns of the host. Weevil feeding on tender acorns caused damaged acorns to fall off the branch and thus reduced acorn yield. It is unclear whether feeding on tender acorns was driven by adult nutritional needs or acted as a "deliberate" acorn-reducing mechanism that led the host to produce fewer but larger acorns. Further studies are required to determine why female *M. ursulus* feed on tender acorns.

Another oak weevil, *Mechoris cumulatus* (Voss), is sympatric with *M. ursulus* in China, and the time of adult occurrence is mostly overlapping in southern China. However, female *M. cumulatus* did not show any oviposition preference for acorn size during our field observations (Z.-Y.Z., unpublished data), which could be attributed to the following two aspects. On one hand, the fruit season of the hosts of *M. ursulus* is much later than that of *M. cumulatus*. Therefore, the period prior for oviposition of *M. ursulus* (~2–3 mo) is much longer than that of *M. cumulatus* (only about 0.5 mo), providing their close emergence time in a year (late May; Z.-Y.Z., unpublished data), and females that emerged earlier with fully developed eggs must oviposit before they die. Choosing relatively larger acorns for oviposition improves offspring performance, however, and the average acorn size of *C. glaucoides* and *Q. franchetii* is smaller than that of *M. cumulatus*-preferred hosts. The difference between *M. ursulus* and *M. cumulatus* oviposition preference may result from coevolution with their hosts (i.e., number of acorns on a branch and acorn size) or the environment (i.e., temperature, precipitation, fruit season, and phenology).

On the other hand, as previously mentioned, the climate of the Central-Yunnan altiplano is characterized by warm and dry winter and spring. Water stress can delay the development of many oak species (Dickson and Tomlinson 1996), and warmer temperatures tend to accelerate insect development up to their tolerance limits (Ratte 1985, Liu and Ye 2010, Ju et al. 2011). The combination of these two factors may help explain the prolonged pre-ovipositional period observed in *M. ursulus* in this area and their observed oviposition preferences.

Acknowledgments

We thank Ms. Sophie Miller and two anonymous reviewers for their valuable comments and improvement of earlier drafts. This study was supported by the National Natural Science Foundation of China (41371514 and 30960061).

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Received 20 July 2013; accepted 6 January 2015.

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