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The Effects of Vegetation Type on *Oedaleus decorus asiaticus* (Orthoptera: Acrididae) Oviposition and Hatching Success

Hongmei Li,[1,2,7,*] Yan Zhang,[1,3] Guangjun Wang,[4] Alyssa Lowry,[5] Wenjiang Huang,[6] Yingying Dong,[6] Suqin Shang,[3,7,*] and Belinda Luke[5]

[1]MARA-CABI Joint Laboratory for Bio-safety, Institute of Plant Protection, Chinese Academy of Agricultural Science, Beijing 100193, China, [2]CABI East Asia, Beijing 100081, China, [3]College of Plant Protection, Gansu Agricultural University, Lanzhou 730070, China, [4]State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Science, Beijing 100193, China, [5]CABI, Egham, TW20 9TY, UK, [6]Key laboratory of Digital Earth Science, Aerospace Information Research Institute, Chinese Academy of Sciences, Beijing 100094, China, and [7]Corresponding author, e-mail: h.li@cabi.org and shangsq@gsau.edu.cn

[*]The authors contributed equally to this work.

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Abstract

Oedaleus decorus asiaticus (Bei-Bienko, 1941) has been regarded as one of the most dominant locusts in the northern grassland, the adjacent area of agriculture and animal farmland, in China. The aims of this study were to investigate the effects of vegetation type on the oviposition behavior of this pest in an open field and the hatching success of the offspring in the following year. The results showed that vegetation type did have a significant effect on whether any egg pods were laid by *O. d. asiaticus*. Once the females laid eggs, vegetation type and cage number had a significant effect on the number of egg pods laid. The highest number of egg pods was found in the *Cleistogenes squarrosa* treatment, followed by *Stipa krylovii* and then *Leymus chinensis*, while the *Artemisia frigida* treatment contained the lowest number of egg pods. The *O. d. asiaticus* eggs laid in *S. krylovii* and *C. squarrosa* treatments had a significantly higher hatching success rate (over 53%) than the other two grasses (below 40%). In short, habitats with *C. squarrosa* and *S. krylovii* grasses are likely to be preferred by ovipositing females, thus population monitoring efforts of *O. d. asiaticus* should focus on these habitats.

Key words: grass type, offspring, egg pod, distribution pattern, grasshopper

In China, grasslands account for more than 40% of the countries land area, and approximately 78% occur in the northern temperate region. These grasslands support a diverse array of plant and animal species and are of significant environmental and economic importance (Sun 2005). In recent years, increasing demand for animal and plant agriculture has put tremendous pressure on these fragile ecosystems. In addition to agriculture, pest species such as grasshoppers and locusts have led to large-scale desertification and degradation of these habitats (Wang et al. 2011). As primary consumers, grasshoppers and locusts compete with farmed animals for food and other resources. One species in particular thrives in relatively dry and highly grazed areas, the *Oedaleus decorus asiaticus* (Bei-Bienko, 1941), which belongs to the Orthoptera (Oedipodidae) order (Kang and Chen 1995). *O. d. asiaticus* accounts for 50–60% of all locusts and grasshoppers found across China's grassland habitats and in some areas, it can account for more than 90% of the local locust and grasshopper population (Chen et al. 2007) and is regarded as the most dominant grasshopper species in the northern grassland and the adjacent area of agriculture and animal farmland (Xu et al. 2005, Gao et al. 2012). The prevalence of *O. d. asiaticus* can partly be attributed to its feeding preference, mainly feeding on *Stipa krylovii*, *Leymus chinensis* (Trin.) Tzvelev, and *Cleistogenes squarrosa* (Trin. ex Ledeb.) Keng, the most dominant plant species in grassland habitats (Kang and Chen 1995).

Locust plagues have been a recurring problem in different parts of Inner Mongolia's grasslands since 2000 (Liu and Guo 2004), and in 2014, 780 km^2 of the 1,133 km^2 of grassland in the Aqi County were seriously affected by an *O. d. asiaticus* outbreak (Sun 2018). The Orthoptera plagues not only accelerated grassland degradation and desertification, but also led to a large loss of foliage posing a serious threat to the local farmers and herdsmen's production and livelihood (Liu et al. 2018). Due to the significant damage that can occur during these outbreaks, being able to predict and prevent the spread occurrence of these locust and grasshoppers has become an urgent requirement to allow farmers to protect grassland ecology and to maintain the sustainable development of agriculture and animal farmland.

Understanding the reproductive behaviors of these locusts plays an important role in predicting and controlling their populations. Oviposition in particular is an important link in the process of insect ontogenesis and plays a vital role in the reproduction of offspring. Choosing suitable oviposition sites is essential to the life history of phytophagous insects, and site choice greatly influences their offspring's chance of survival. Not only should the oviposition site provide protection but also potential food resources for the newly emerged larvae to aid their development during their most vulnerable stages (Zhang and Ji 1994, Li et al. 2012). For example, insects that lay their eggs in the soil, like *O. d. asiaticus* greatly reduce their eggs exposure to certain harmful factors such as desiccation, predators, and parasitoids. This behavior ensures that offspring have a relatively stable environment for growth and development (Ji et al. 2006).

A number of factors, both abiotic and biotic, affect the oviposition behavior of locusts and grasshoppers. Vegetation type in particular has been shown to have a significant impact on female oviposition. You and Ma (1964) found that *Locusta migratoria manilensis* (Meyen 1835) (Orthoptera: Acrididae) females preferred to oviposit in habitats with *Phragmites australis* (Cav.) Trin. ex Steud (Poales: Poaceae), *Imperata cylindrica* (L.) Raeusch (Poales: Poaceae) and *Aeluropus sinensis* (Debeaux) Tzvelev (Poales: Poaceae), but not *Artemisia halodendron* Turcz. ex Besser (Asterales: Compositae). Whereas the solitary *Schistocerca gregaria* (Forskål, 1775) (Orthoptera: Catantopidae) females preferred to oviposit in the sites with *Heliotropium* spp. (~66%) and millet (~32%) seedlings. Furthermore, vegetation type has also been shown to influence the number of eggs female locust and grasshopper lay. For example, Qin et al. (1957) showed that *L. m. manilensis* laid the most eggs when fed on *Zea mays* L. (Poales: Poaceae) compared with *Triticum aestivum* L. (Poales: Poaceae) and *Setaria italica* (L.) P.Beauv. (Poales: Poaceae). Solitary nymphs were also shown to prefer to feed on those plants (Bashir et al. 2000).

While regions with *L. chinensis*, *S. kirschnei*, *S. grandis*, and *C. squarrosa* have been demonstrated to be suitable habitats for *O. d. asiaticus* (Du et al. 2018), only a limited number of studies have specifically been carried out to confirm habitat suitability in relation to oviposition behavior of this species. One such study was conducted by Zhang et al. (2020) observing the effects of different soil types and soil moisture content on egg hatching of *O. d. asiaticus*. This study aims to further the work conducted by Zhang et al. by investigating whether *O. d. asiaticus* can discriminate among vegetation types in field conditions. For this experiment the grasses, *Artemisia frigida*, *C. squarrosa*, *L. chinensis*, and *S. krylovi* were used as treatment groups, as they reflect some of the most dominant grass species found in China's grassland habitats. The results of this study may clarify the habitat characteristics of the optimal sites for *O. d. asiaticus* oviposition and be used to improve the allocation of resources for monitoring surveys and population predictions.

Materials and Methods

Grasshoppers

The nymphs of *O. d. asiaticus* were captured by sweeping net close to 307 Provincial Highway in Xilinhot City, Xilingol League, Inner Mongolia (44°04′N, 116°27′E). There were approximately 3,500 nymphs captured in mid-July 2019. The captured grasshoppers were reared in three cages with iron frames and wire mesh (4 × 2 × 2 m) and were located in natural field conditions, with 1,000 nymphs in each cage. The cages were set in the Key Observation and Experiment Station of Pest Control in Xilingol Grassland of the Ministry of Agriculture and Rural Affairs, China (43°95′N, 116°00′E).

Oviposition Experiment

Four dominant experimental grass species, *A. frigida*, *C. squarrosa*, *L. chinensis*, and *S. krylovi*, with healthy growth and similar size, were carefully transplanted from the field into 150 white plastic pots (13.5 × 13.5 × 14.5 cm) for each grass species and watered daily until they became established (about 7 d). Three identical cages were then set up. A total of 48 pots of grass seedlings were placed in each cage consisting of 12 pots for each kind of grass.

In total, 192 (48 × 4 grass species) pots of grass seedlings were placed in each wire cage before oviposition. The number of egg pods and eggs was counted, and the depth of egg pods was measured for each pot after the grasshoppers died (approximately 1 mo). The experiment was conducted from 18 July to 13 August 2019.

Hatching Ratio

The egg pods from oviposition experiment with soil were labeled by grass species and stored in fridge at 4°C. Based on the experimental methods of Hu et al. (2008), Sun et al. (2010), and Ren et al. (2015), the brown calcic soil was dried in the oven at 120°C for a minimum of 2 h. After cooling the soil, sterilized water was added to obtain 15% soil moisture content. Plastic cups (height = 12 cm, diameter = 8 cm), were first filled with about 2/3 of the hydrated soil, about 100 eggs were laid on the soil before being covered with a further 2.5-cm soil. The cups were sealed with plastic film and rubber bands to maintain the soil moisture content and kept at artificial chamber at 28 ± 1°C, RH = 60 ± 5%. The pots were stored in the dark (Zhang et al. 2020). There were three cups for each grass. The cup incubators were checked daily to see if any nymphs had hatched. The number of nymphs and the hatching date were recorded until there are no further nymphs hatched for four consecutive days. The experiment was conducted from 1 April to 13 May 2020.

Statistical Analysis

Statistical analyses were performed using R version 4.0.2 (R Development Core Team 2020), using packages MASS (Venables and Ripley 2002), multcomp (Hothorn et al. 2008), emmeans (Russell 2020), car (Fox and Weisberg 2019), and ggplot2 (Wickham 2009). Generalized linear models were used to analysis what factors influenced aspects of *O. d. asiaticus* oviposition and hatching success, with the appropriate distribution being determined by checking the model assumptions. A model was developed to analyze each of the following dependent variable; the proportion of eggs that successfully hatched, the total number of egg pods laid (Poisson distribution), the total number of eggs laid, the average number of eggs laid within eggs pods (negative binomial distribution), the depth of egg pods from the top of the soil, and the depth of egg pods from the bottom of the pot (Gaussian distribution). Vegetation type, cage number, and all possible interactions were set as the independent variables. A stepwise regression (both forward and back) was then used to determine the minimum adequate model in each case. An analysis of deviance was conducted on the minimum adequate model to determine the overall effect of the remaining independent variables, followed by a Tukey's post hoc test to further investigate any significant results.

Results

Total Number of Egg Pods

The analysis of deviance indicated that vegetation type had a significant effect on the total number of egg pods laid (analysis of variance [ANOVA], $\chi^2(3) = 60.89$, $P < 0.01$). The total number of egg pods was differing significantly between all vegetation types ($P < 0.01$), except for *L. chinensis* and *A. frigida* ($P = 0.71$). Further analysis showed that the *C. squarrosa* replicates contained the greatest number of egg pods with a total of 109, followed by *S. krylovii* with 61, followed by the *L. chinensis* and *A. frigida* replicates with only 21 and 20 egg pods, respectively (Fig. 1).

Cage number was also found to have a significant effect on the total number of egg pods laid (ANOVA, $\chi^2_{(2)} = 22.734$, $P < 0.01$). With cage 3 containing the highest number of egg pods (99), followed by cage 2 (69) and lastly cage 1 containing only 43 egg pods (Fig. 2).

The interaction between vegetation type and cage number was also significant (ANOVA, $\chi^2_{(6)} = 22.362$, $P < 0.01$, Fig. 3). Further analysis showed that females from all cages laid the greatest number of egg pods in *C. squarrosa* pots compared with the other vegetation types.

Total Number of Eggs

The analysis of deviance indicated that only vegetation type (ANOVA, $\chi^2_{(3)} = 24.76$, $P < 0.01$, Fig. 4) and the interaction between vegetation type and cage number (ANOVA, $\chi^2_{(6)} = 18.86$, $P < 0.01$, Fig. 5) had a significant effect on the total number of eggs laid by *O. d. asiaticus*. *Cleistogenes squarrosa* replicates had the highest number of eggs (2,228), followed by *Stipa krylovii* (1,085), then *L. chinensis* (396), with *A. frigida* (385) having the lowest. However, the average number of eggs per egg pod did not differ significantly between vegetation types.

Average Number of Eggs Within Egg Pods

The statistical analyses indicated that no factor had a significant effect on the number of eggs laid within each egg pod. The average number of eggs per pod was 19.2.

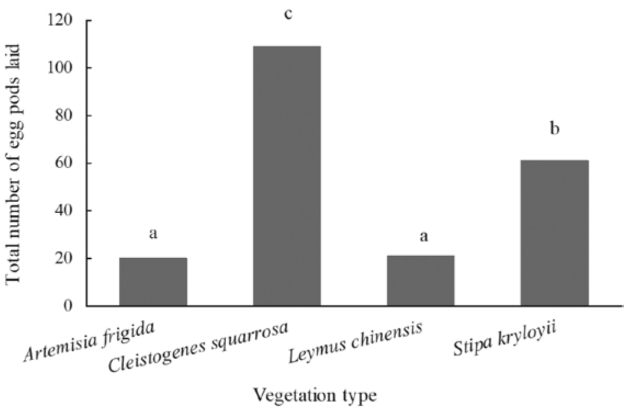

Fig. 1. The total number of egg pods laid in each vegetation type. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$).

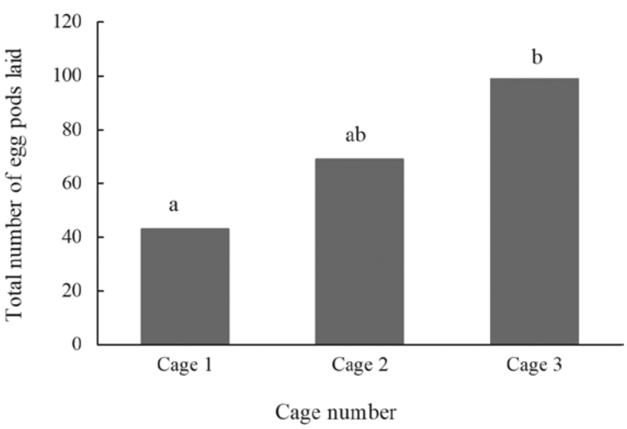

Fig. 2. The total number of egg pods laid in each cage. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$).

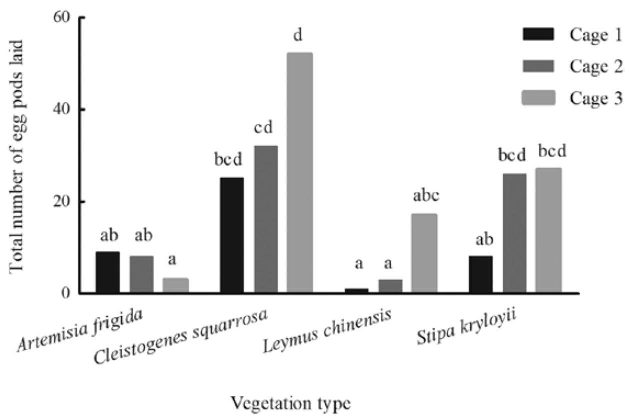

Fig. 3. The total number of egg pods present in each vegetation type within each cage. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$).

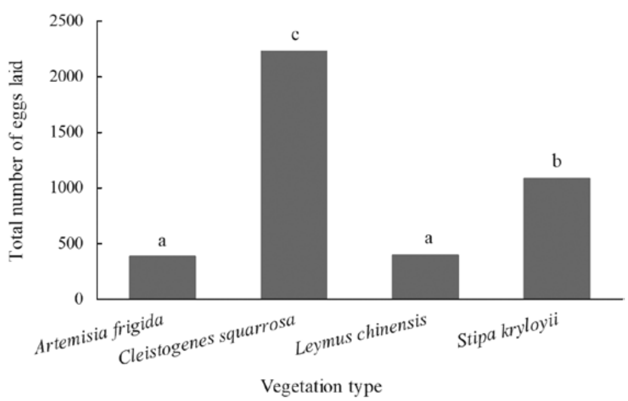

Fig. 4. The total number of eggs laid in each vegetation type. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$).

The Hatching Success of Eggs From Different Vegetation

Vegetation type had a significant effect on the proportion of *O. d. asiaticus* eggs that successfully hatched (ANOVA, $\chi^2_{(3)} = 25.526$, $P < 0.01$, Fig. 6). A Tukey post hoc test indicated that a greater proportion of the eggs hatched when laid in *S. krylovii* (53.37 ± 2.54%) and *C. squarrosa* (53.33 ± 2.90%) habitats when compared with *L. chinensis* and *A. frigida* habitats ($P < 0.05$).

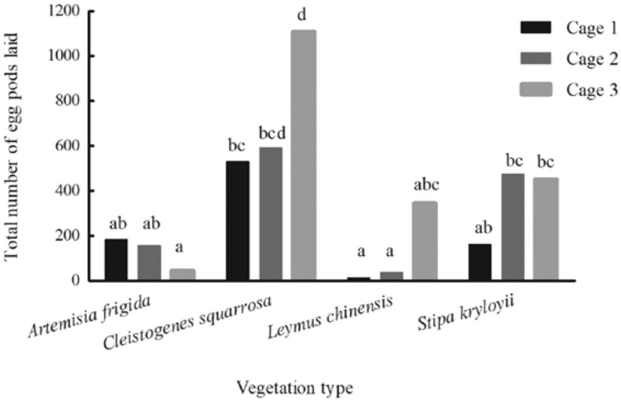

Fig. 5. The total number of eggs laid in each vegetation type in each cage. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$).

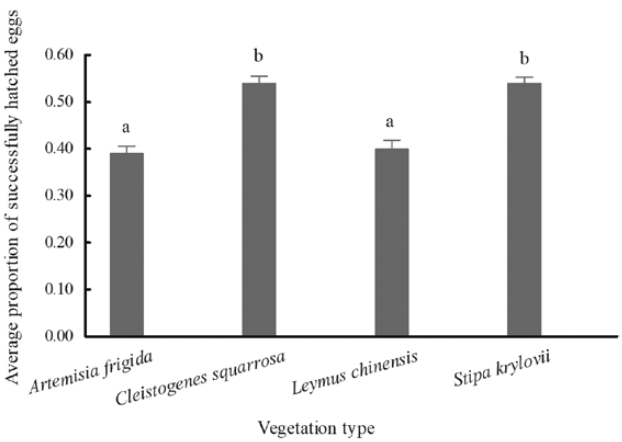

Fig. 6. The average ratio of successfully hatched eggs from within each vegetation type. Letters above bars indicate significant difference (Tukey's HSD, $P < 0.05$). Error bars represent SE.

Depth that the Egg Pods Were Laid in the Soil

Egg pods of *O. d. asiaticus* were longest in *C. squarrosa*, with 1.52 ± 0.03 cm, followed by *S. krylovii* with 1.47 ± 0.04 cm. The shortest egg pods were in *L. chinensis* and *A. frigida*, which were 1.42 ± 0.05 cm and 1.42 ± 0.07 cm, respectively, but there was no significant difference among the four vegetations ($P > 0.05$). The average depth of the top of the egg pods and the average depth of the bottom of the egg pods were the deepest in *C. squarrosa*, followed by *S. krylovii*, and were shallower in *L. chinensis* and *A. frigida*, respectively, but there was no significant difference in the depth of the egg pods among the four grass types (Table 1, $P > 0.05$).

Discussion

The results of this study indicate that vegetation had a significant effect on the oviposition behavior and hatching success of *O. d. asiaticus*. Females laid more egg pods in habitats with *C. squarrosa*, followed by *S. krylovii*, then *L. chinensis* and *A. frigida*, with no significant difference in preference between the latter two. Similarly, eggs laid in *C. squarrosa* and *S. krylovii* habitats had a greater proportion of eggs hatch in the following year compared with *L. chinensis* and *A. frigida* habitats. This is concurrent with a study conducted by Cui et al. (2019), which found that *O. d. asiaticus* preferred to feed on *C. squarrosa* and *S. krylovii*, but seldom fed on *L. chinensis*. This inherent feeding preference would provide more potential opportunities for females to choose the above habitats for oviposition. This partiality according to Cease et al. (2012) is likely linked to *O. d. asiaticus* preference for feeding on plants with a low nitrogen content. As contrary to popular belief, that increased plant nitrogen levels should be beneficial to herbivore activity, Cease et al. (2012) found that diets high in nitrogen decreased the size and viability of *Oedaleus asiaticus*. The high nitrogen content, may in turn have led to decreased egg viability.

Although vegetation had a significant effect on the number of egg pods laid by females and the proportion of eggs that hatched in the following year, it did not affect the number of eggs within each egg pod, suggesting that females invest the same amount of energy in each reproductive attempt regardless of vegetation. However, the number of eggs that successfully hatched in habitats with *C. squarrosa* and

Table 1. The length and depth of *Oedaleus decorus asiaticus* egg pod in different vegetation

Type	Vegetation	Average (cm)	Minimum value (cm)	Maximum value (cm)
The length of egg pods	*Leymus chinensis*	1.42 ± 0.05 a	1.1	1.9
	Stipa krylovii	1.47 ± 0.04 a	0.8	2.6
	Cleistogenes squarrosa	1.52 ± 0.03 a	0.8	2.6
	Artemisia frigida	1.42 ± 0.07 a	0.9	2.1
The top depth of egg pods	*Leymus chinensis*	2.37 ± 0.09 a	1.4	3.1
	Stipa krylovii	2.45 ± 0.06 a	1.5	3.5
	Cleistogenes squarrosa	2.47 ± 0.04 a	1.5	3.8
	Artemisia frigida	2.25 ± 0.12 a	1.5	4.0
The bottom depth of egg pods	*Leymus chinensis*	3.79 ± 0.12 a	2.9	5.0
	Stipa krylovii	3.92 ± 0.07 a	2.5	5.1
	Cleistogenes squarrosa	3.99 ± 0.05 a	2.6	5.4
	Artemisia frigida	3.66 ± 0.15 a	2.6	5.6

Data in the table are means ± SE. There was no significant difference in the length of egg pod in different vegetation.

S. krylovii was significantly greater than that of *L. chinensis* and *A. frigida*, indicating that although the quantity of eggs laid does not differ significantly between vegetations, the quality of eggs does. This difference in fecundity could be the result of dietary stress experienced by the females before oviposition. Numerous studies have found that secondary metabolites in grasses such as *A. frigida* caused significant stress to *O. d. asiaticus* grasshoppers. The dietary stress resulted in lower growth, size, development, survival, and fecundity in comparison to those fed on *C. squarrosa* and *S. krylovii* (Huang et al. 2017, Cui et al. 2019). Vegetation was found not to significantly affect the depth at which egg pods were laid; however, on average, the egg pods laid in *C. squarrosa* and *S. krylovii* were deeper in the soil comparing the other two type of grasses. Egg pod depths ranged from 1.5 to 4.0 cm from the top of the soil and from 2.6 to 5.6 cm from the bottom of the pots.

Despite each cage being set up as an identical replicate, cage was found to have a significant effect on both the total number of egg pods and eggs within the egg pods. The significant difference between cages could be by chance. However, one possible explanation could be that this is the result of the sweep net method used to capture the nymphs of *O. d. asiaticus*. Each cage was filled consecutively with cage 1 being filled first. Thus, it is likely that individuals caught first were of a lower quality/older than individuals caught later and hence could not jump away from the sweep net as quickly as the more robust grasshoppers.

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