

Food-plant choice of seven dominant grasshopper species in the Xinjiang grasslands

JIN-LONG REN^{1*}, WEN-JING KANG^{1*}, JIN-XING LI¹, XI JIN², KE-XIN LI¹, LI ZHAO¹

1 Key Laboratory of the Pest Monitoring and Safety Control on the Crop and Forest, College of Agronomy, Xinjiang Agricultural University, Urumqi 830052, China.

2 Grassland Workstation in Bole, Bortai Mongol Autonomous Prefecture, Bole 833400, China.

Corresponding authors: Li Zhao (zlym57@sohu.com), Jin-Long Ren (rjlinsect@163.com)

Academic editor: Editor | Received 7 August 2023 | Accepted 11 December 2023 | Published 13 May 2024

<https://zoobank.org/47C4A29E-747D-47D9-A1B7-7E0020120C8B>

Citation: Ren J-L, Kang W-J, Li J-X, Jin X, Li K-X, Zhao L (2024) Food-plant choice of seven dominant grasshopper species in the Xinjiang grasslands. Journal of Orthoptera Research 33(1): 157–168. <https://doi.org/10.3897/jor.33.110690>

Abstract

Feeding habits and competitive interactions among dominant grasshopper species in the Xinjiang grasslands (China) were studied under natural conditions through microscopic analyses of insect crop contents. Sex-specific and interindividual differences in feeding habits and interspecific competition were investigated. Analyses of ecological niche width and overlap revealed potential competition among grasshoppers. The results showed significant difference in the sex-specific variations in the feeding habits of the seven grasshoppers; sex-specific variations in feeding range and preferred plants were observed, with females feeding more extensively on host plants, and female and male adults choosing to feed on different plant species. Individuals of all seven grasshoppers showed different degrees of dietary variance, with oligophagous grasshoppers (*Oedaleus decorus* males, *Dericorys annulata*, and *Bryodema gebleri* males) showing a smaller degree of individual dietary variance than polyphagous grasshoppers (*Oedipoda caerulescens*, *Calliptamus coelesyriensis* females, *Calliptamus barbarus*, and *Notostaurus albicornis*); *Calliptamus coelesyriensis* and *Notostaurus albicornis* showed the greatest individual variance in their diets. *Oedaleus decorus*, *Bryodema gebleri*, and *Calliptamus barbarus* consumed primarily Poaceae and exhibited varying food-plant choice. For example, *Oedaleus decorus* was observed to have high-preference feeding for *Poa annua*, *Bryodema gebleri* for *Stipa capillata*, and *Calliptamus barbarus* for *Setaria viridis*. *Dericorys annulata* fed primarily on Amaranthaceae, *Notostaurus albicornis* fed primarily on Poaceae and Amaranthaceae, and *Oedipoda caerulescens* fed primarily on Asteraceae. *Calliptamus barbarus* exhibited strong interspecific competition with *Oedaleus decorus* and *Calliptamus coelesyriensis*, and *Bryodema gebleri* demonstrated the strongest interspecific competition with all six other species. Considering the influence of sex on interspecific competition among grasshoppers enhances our understanding of interspecific competitive relationships.

Keywords

caelifera, diet, intraspecific competition, individual variation, sex

Introduction

Grassland ecosystems are among the most significant on Earth (Nan 2022) and provide essential benefits for human welfare and economic growth (WRI 1986). In China, grasslands cover approximately 40% of the land area and are therefore a dominant feature of the national landscape. The northern grassland ecosystems of China play crucial roles in maintaining the region's environment and supporting diverse plant and animal species (Kang et al. 2007); they also contribute to socio-economic development.

Xinjiang, located in the western part of China's northern grasslands, has a grassland area of 57.7 million hectares, making it the region with the third-largest area of grasslands in China. The province is among those with the richest grassland resources in China (Muhetaer 2000). Grasshoppers are important components of grasslands, as they compete with domestic animals for food resources and affect the productivity of grasslands (Kang et al. 2007). In China, grasshoppers are considered significant pests affecting agriculture and livestock production. Grasshoppers, along with droughts and floods, are known to cause major natural disasters in the agricultural and livestock production in China (Zhang 2011). Thus, studying the food-plant choices of grasshoppers may aid in the development of ecological management methods for preventing grasshopper infestation. For example, such methods could include growing plants that grasshoppers do not prefer to feed on in areas prone to grasshopper plagues (Zhang et al. 2020).

Several dominant species of grassland grasshoppers, including *Oedaleus decorus*, *Oedipoda caerulescens*, *Bryodema gebleri*, *Calliptamus coelesyriensis*, *Calliptamus barbarus*, *Dericorys annulata*, and *Notostaurus albicornis*, have been identified in Xinjiang (Chen 1981). Investigating their feeding habits may facilitate the development of more precise and effective grasshopper control strategies. Analysis of the trophic ecological niche of grassland grasshoppers

* These authors contributed equally to this work.

is essential for understanding the structure, diversity, and stability of grasshopper communities (Kang and Chen 1994a).

Food preference plays a crucial role in determining herbivores' diets and spatial distributions (Ibanez et al. 2013a). Various research methods have been used to study grasshopper feeding, including direct observation, analyzing carbon isotope ratios (Fry et al. 1978), microscopic analyses of feces/frass (Tyrkus and Gangwere 1970), microscopic analyses of crop contents (MACC) (Ueckert and Hansen 1971, Joern 1979, Joern 1983, Kang and Chen 1994b), and DNA barcoding techniques (Ibanez et al. 2013a, McClenaghan et al. 2015). Among these methods, MACC remains a commonly used approach in grasshopper feeding analysis because of its precision, efficiency, low cost, and simplicity of use (Gall et al. 2003, Liu et al. 2007, Wang and Ma 2009, ELELA et al. 2010).

Research on grasshopper species using MACC has been conducted in Inner Mongolia (Kang and Chen 1994a, b), Gansu (Liu et al. 2007), and Zhejiang (Wang and Ma 2009) in China. However, Xinjiang, where approximately one-sixth of all known grasshopper species in China are found, remains understudied. Moreover, previous studies using caging methods have only sporadically investigated the seven grasshopper species studied herein. For example, Wang (2007) examined the feeding habits of *Oedaleus decorus*, *Calliptamus coelesyriensis*, and *Bryodema gebleri* (Wang 2007), whereas Huang (1995) explored the food-plant species for *Oedaleus decorus* and *Bryodema gebleri* (Huang 1995). However, the caging method used in those studies can be influenced by the level of observed detail and observation time, potentially resulting in significant errors in experimental data. This method often captures artificial forced feeding rather than the independent selection of food by grasshoppers in their natural environment, thereby inaccurately representing grasshoppers' feeding behavior.

Insects exhibit distinct patterns of host-plant feeding that vary between the sexes and among individuals (Schoonhoven et al. 2005). To analyze the adaptive feeding behavior of herbivorous insects in heterogeneous environments, it is necessary to understand the variation in the feeding strategies of herbivorous insects in relation to feeding preferences based on sex (Unsicker et al. 2008). Although experimental evidence has revealed dietary disparities between males and females (Maklakov et al. 2008, Ng et al. 2019), empirical support in natural settings remains deficient (Lan et al. 2021). It is commonly assumed that individuals are often specialized and that population-level polyphagy in many insect species is a result of specialization on many different resources by individuals within the population (Singer 1983, Via 1984, Halima et al. 1985, Braker 1987, Howard et al. 1994). There have been few studies on the individual feeding patterns of polyphagous Orthopteran insects (Howard 1993, 1995, Howard et al. 1994); in particular, inter-individual grasshopper feeding characteristics are unknown, and resolution of this issue will contribute to the understanding of generalized feeding patterns in the context of Orthopteran evolution (Howard 1995).

In this study, the grasshoppers were collected in July of 2018, and predation observations and analysis were conducted from 2019–2022. We hypothesized that the magnitude of inter-individual feeding differences is related to the range of grasshopper feeding. For this reason, we selected three oligophagous grasshoppers and four polyphagous grasshoppers known to be present in Xinjiang, China, investigated their feeding status under natural conditions, and utilized crop inclusion microanalysis to study the feeding differences between the two sexes in each species and among individuals and species. We also analyzed the feeding frequency, ecological niche width, and degree of overlap to clarify the feeding status of the sexes, individuals, and species among the seven grasshoppers..

Materials and methods

Study site and species.—Based on an examination of the grasslands in the Bozhou region of Xinjiang, China, we selected six natural grassland study sites that are not artificially managed. Collecting was done in the summer of 2018. In each sample plot, a net was swung 100 times in each of four directions (east, south, west, and north); each net was spaced 2 m apart. We identified grasshoppers visually, and 10 females and 10 males of each species were randomly selected and collected for crop inclusion microanalysis. The present study reports on grasshoppers from seven species belonging to two families (Acrididae and Dericorythidae) and three subfamilies (Oedipodinae, Calliptaminae, and Gomphocerinae) of the Acrididae. The species collected were *Oedaleus decorus*, *Oedipoda caerulea*, and *Bryodema gebleri* from the Oedipodidae; *Calliptamus coelesyriensis*, and *Calliptamus barbarus* from the Calliptaminae; *Dericorys annulata* from the Dericorythidae; and *Notostaurus albicornis* from the Gomphocerinae. Table 1 provides details of the vegetation growth found at the collection sites. We used visual estimation to record vegetation cover in six sample plots and designated the species of the community that was the most numerous, the largest in size, and had the greatest impact on the habitat as the dominant species in the community.

Dietary analysis.—The experiment was conducted using adult grasshoppers immediately killed with a 75% ethanol solution and transported to the laboratory. Microscopic analysis of the grasshoppers' crop contents was then conducted to determine food choices. By comparing the plant fragments collected from the crops with those obtained from voucher specimens collected in the study area (Liu et al. 2007), we were able to identify the food plant species that had been consumed.

Data analysis.—The relative frequency of feeding (RFN) was calculated using Li's (1983) measure:

$$(RFN)_x = \frac{X}{\sum x}$$

where X is the number of times in which a plant is found in an individual insect's anatomical samples and $\sum x$ is the total number of times in which all plants are found in an individual insect's crop.

Grasshopper feeding was classified into four categories according to RFN values: RFN > 0.5 was considered "high-preference feeding," RFN of 0.5–0.25 was considered "preference feeding," RFN of 0.25–0.024 was considered "seldom feeding," and RFN < 0.024 was considered "occasional feeding." The degree of grasshoppers' preference for feeding on plants was defined accordingly (Li et al. 1983).

To determine species niche breadth, we used Levin's measure (1968):

$$B = \frac{1}{\sum p_i^2}$$

where B represents Levin's measure of food niche breadth and p_i denotes the proportion of the food i consumed by a species among all foods consumed.

We used Schoene's measure (1970) to calculate species niche overlap:

$$C_{ij} = 1 - \frac{1}{2} \sum_j |p_{ij} - p_{ij}|$$

Table 1. Basic information on insect sources (gathered in 2018).

Family	Subfamily	Grasshoppers				Acquisition time (Y.M.D)	Dominant species	Plants	
		Species	Collection site (city)	Relative abundance in the point	Vegetation cover of the point (%)			Non-dominant species	
Acrididae	Oedipodinae	<i>Oedaleus decorus</i> (Germar, 1825)	Ku Si Mu Qie Ke (Bole)	68.2%	2018.7.26	<i>Seriphidium borotalense</i>	<i>Anabasis</i> sp., <i>Nanophyton erinaceum</i> , <i>Stipa capillata</i>	45%–50%	
		<i>Bryodema gebleri</i> (Fischer von Waldheim, 1836)	Tuo Si Gou (Wenquan)	34.13%	2018.7.31	<i>Nanophyton erinaceum</i> , <i>Seriphidium borotalense</i>	<i>Anabasis</i> sp., <i>Astragalus membranaceus</i> , <i>Carex</i> sp., <i>Nanophyton erinaceum</i> , <i>Peganum harmala</i> , <i>Polygonum aviculare</i> , <i>Stipa capillata</i>	15%–20%	
		<i>Oedipoda caerulea</i> (Linnaeus, 1758)	Xiao Hai Zi (Jinghe)	13.4%	2018.7.25	<i>Caragana sinica</i> , <i>Festuca ovina</i> , <i>Stipa capillata</i> , weeds	<i>Achillea millefolium</i> , <i>Artemisia frigida</i> , <i>Artemisia sieversiana</i> , <i>Avena sativa</i> , <i>Berberis amurensis</i> , <i>Cirsium arvense</i> , <i>Cirsium arvense</i> , <i>Inula rhizocephala</i> , <i>Juniperus sabina</i> , <i>Leontopodium leontopodioides</i> , <i>Neotrinia splendens</i> , <i>Poa annua</i> , <i>Polygonum aviculare</i> , <i>Setaria viridis</i> , <i>Taraxacum mongolicum</i> , <i>Urtica fissa</i>	75%–80%	
	Calliptaminae	<i>Calliptamus coelesyriensis</i> Giglio-Tos, 1893	Xiaoyingpan 1 Ranch (Bole)	43.82%	2018.7.24	<i>Seriphidium borotalense</i>	<i>Atraphaxis spinosa</i> , <i>Ceratocarpus arenarius</i> , <i>Lactuca tatarica</i> , <i>Peganum harmala</i> , <i>Poa annua</i>	15%–20%	
		<i>Calliptamus barbarus</i> (Costa, 1836)	Ranch No. 1, Qingxiang, Yamatan (Bole)	21.02%	2018.7.24	<i>Seriphidium borotalense</i>	<i>Caragana sinica</i> , <i>Ceratocarpus arenarius</i> , <i>Nanophyton erinaceum</i> , <i>Peganum harmala</i> , <i>Poa annua</i> , <i>Setaria viridis</i>	15%–20%	
		<i>Notostaurus albicornis</i> (Eversmann, 1848)	Ranch No. 1, Qingxiang, Yamatan (Bole)	41.42%	2018.7.24	<i>Seriphidium borotalense</i>	<i>Caragana sinica</i> , <i>Ceratocarpus arenarius</i> , <i>Nanophyton erinaceum</i> , <i>Peganum harmala</i> , <i>Poa annua</i> , <i>Setaria viridis</i>	15%–20%	
Dericorythidae		<i>Dericorys annulata</i> (Fieber, 1853)	Alashankou Reservoir (Alashankou)	39.37%	2018.7.23	<i>Anabasis cretacea</i> , <i>Kali collinum</i> , <i>Seriphidium borotalense</i>	<i>Bassia prostrata</i> , <i>Haloxylon ammodendron</i> , <i>Krascheninnikovia ceratoides</i> , <i>Neotrinia splendens</i> , <i>Stipa capillata</i> , <i>Suaeda glauca</i>	10%–15%	

where C_{ij} represents the degree of niche overlap between species i and h , P_{ij} is the number of times in which plant i is found among all anatomical samples of insect species j , and P_{ik} is the number of times in which plant i is found among all anatomical samples of insect species k . C_{ij} varies from 0 to 1, with 0 representing no overlap and 1 representing complete overlap; $C_{ij} > 0.6$ is generally considered biologically significant (Colwell 1971, Li Yunkai et al. 2021).

Overlap among food ecological niches was defined by two or more species with similar ecological niches sharing or competing for common resources while living in the same space. The degree of niche overlap was expressed by the C_{ij} index (Colwell 1971).

Statistical analysis.—We used SPSS (version 19; SPSS Inc.) on a personal computer for all statistical analyses. To test whether male and female grasshoppers differ in feeding ecology, we performed a multivariate analysis of variance (MANOVA) with sex as the sole factor and host plant as the dependent variables (Vincent 2006). We used Kendall's coefficient of concordance to test for differences in feeding among grasshopper individuals (Howard 1995). We performed analysis of variance (ANOVA) on the width of ecological niches and used a t-test to investigate differences between the sexes.

Results and analysis

Dietary composition.—The seven grasshopper species had ingested a total of 33 distinct botanical species (Figs 1, 3). Notably, *Notostaurus albicornis* showed the greatest breadth of food sources, consuming 15 species; in contrast, *Dericorys annulata* consumed only five species. Poaceae, Fabaceae, Asteraceae, and Amaranthaceae were consumed by nearly all grasshoppers across the seven families, whereas Nitrariaceae, Caprifoliaceae, and Tamaricaceae were consumed by only one or two grasshopper species (Figs 2, 3). Among

the 33 host plants, we identified five plants (*Poa annua*, *Setaria viridis*, *Caragana sinica*, *Stipa capillata*, and *Seriphidium borotalense*) fed on by five or six grasshopper species; in contrast, six plants (*Festuca ovina*, *Suaeda glauca*, *Ceratocarpus arenarius*, *Anabasis cretacea*, *Bassia prostrata*, and *Artemisia sieversiana*) were fed on by three grasshopper species. The remaining 22 plant species were consumed by only one or two grasshopper species (Fig. 3).

Food preference.—**Sex variation.** As indicated in Figs 1, 2, we observed little difference in the diets between sexes for *Oedaleus decorus*, *Dericorys annulata*, *Oedipoda caerulea*, and *Notostaurus albicornis*. However, two significant differences in dietary composition were observed between sexes for *Calliptamus coelesyriensis*, *Calliptamus barbarus*, and *Bryodema gebleri*. First, females of these species consumed more host plant species than males; for example, *Bryodema gebleri* females consumed plants from 11 species across five families, whereas males consumed only seven species across three families. Similarly, *Calliptamus coelesyriensis* females consumed plants from eight species across five families, whereas males consumed plants from only two species in two families. Finally, *Calliptamus barbarus* females consumed plants from nine species across four families, whereas males consumed plants from seven species across four families. Second, the main plants consumed by each sex varied among species. *Bryodema gebleri* females fed primarily on Amaranthaceae (46.50%), whereas males favored Poaceae (93.12%); *Calliptamus coelesyriensis* females fed primarily on Nitrariaceae (57.33%), whereas males fed predominantly on Amaranthaceae (56.25%); and *Calliptamus barbarus* females consumed primarily Poaceae (82.44%), whereas males consumed primarily Amaranthaceae (56.20%).

Significant differences in high-preference feeding on plants between male and female adults were observed in the seven

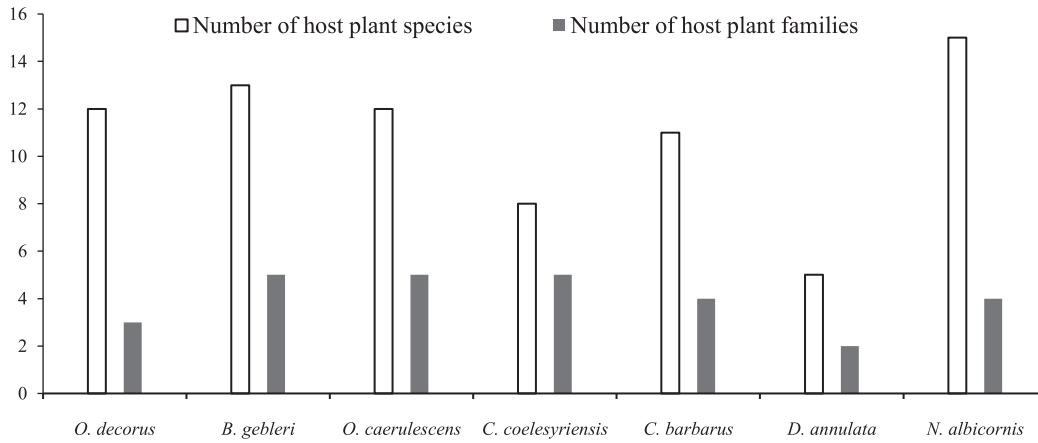


Fig. 1. Number of plants fed on by seven grasshopper species.

grasshopper species (Fig. 3). For example, *Oedaleus decorus* females showed high-preference feeding on *Poa annua* (RFN = 0.51, as below) and did not feed on *Stipa capillata*, whereas opposite findings were observed for males, which showed high-preference feeding on *Stipa capillata* (0.76) but not on *Poa annua*. Similarly, *Oedipoda caerulescens* females exhibited high-preference feeding on *Artemisia scoparia* (0.72) but did not feed on *Artemisia sieversiana*, whereas males displayed opposite behavior, in which they preferred to feed on *Artemisia scoparia* (0.38) and *Artemisia sieversiana* (0.25). Among the other species, *Calliptamus coelesyriensis* females showed high-preference feeding on *Peganum harmala* (0.57), whereas males preferred feeding on *Ceratocarpus arenarius* (0.56). In addition, *Calliptamus barbarus* females showed high-preference feeding on *Setaria viridis* (0.57), whereas males showed high-preference feeding on *Ceratocarpus arenarius* (0.56). Finally, *Notostaurus albicornis* females preferred feeding on *Bassia prostrata* (0.36), whereas males preferred feeding on *Anabasis cretacea* (0.27).

Through MANOVA on the RFN of botanical specimens consumed by both sexes of grasshoppers, it was established that *Oedaleus decorus* females fed significantly more strongly on *Psathyrostachys juncea* and *Poa annua* than their male counterparts ($P = 0.002, 0.000 < 0.01$), and females fed significantly less on *Stipa capillata* than their male counterparts ($P = 0.000 < 0.01$). *Bryodema gebleri* females fed significantly more strongly on *Suaeda glauca* than males ($P = 0.004 < 0.01$), but significantly less on

Stipa capillata than males ($P = 0.000 < 0.01$). *Oedaleus caerulescens* females fed significantly more strongly on *Artemisia scoparia* than males ($P = 0.009 < 0.01$), and females fed significantly less on *Artemisia sieversiana* than males ($P = 0.005 < 0.01$). *Calliptamus coelesyriensis* females fed significantly more strongly on *Caragana sinica* and *Peganum harmala* than males ($P = 0.007 < 0.01$ and $P = 0.026 < 0.05$, respectively) but significantly less on *Ceratocarpus arenarius* than males ($P = 0.000 < 0.01$). *Calliptamus barbarus* females fed significantly more on *Setaria viridis* than males ($P = 0.009 < 0.01$) but significantly less on *Festuca ovina*, *Ceratocarpus arenarius* and *Caragana sinica* than males ($P = 0.035 < 0.05$ and $P = 0.002, 0.002 < 0.01$, respectively). *Dericorys annulata* females fed significantly less on *Bassia prostrata* than males ($P = 0.042 < 0.05$). *Notostaurus albicornis* females fed significantly more on *Bassia prostrata* than males ($P = 0.006 < 0.01$) but significantly less on *Ceratocarpus arenarius*, *Stipa capillata* and *Seriphidium borotalense* than males ($P = 0.026, 0.020 < 0.05$ and $P = 0.003 < 0.01$, respectively).

Interindividual variation. The individual feeding habits of the seven species of grasshoppers are shown in Fig. 5. As shown in Fig. 4, the P values for the seven species of grasshoppers were all greater than 0.05, indicating that there was no significant consistency among individuals. This means that there are different degrees of feeding differences among the individuals of the seven species of grasshoppers: the P values of the seven species of grasshoppers

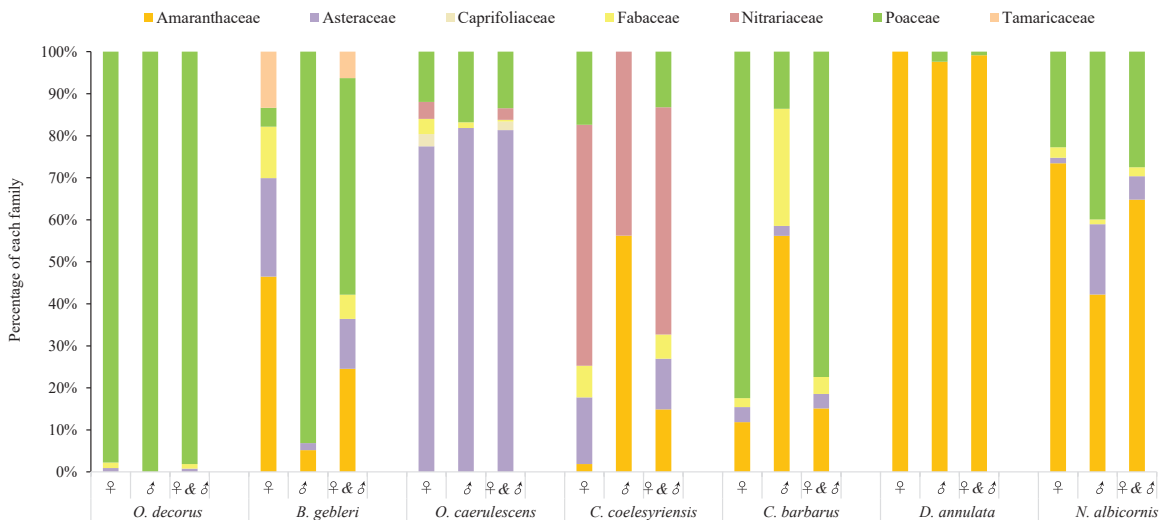


Fig. 2. Percentage of each host plant family eaten by the seven grasshopper species.

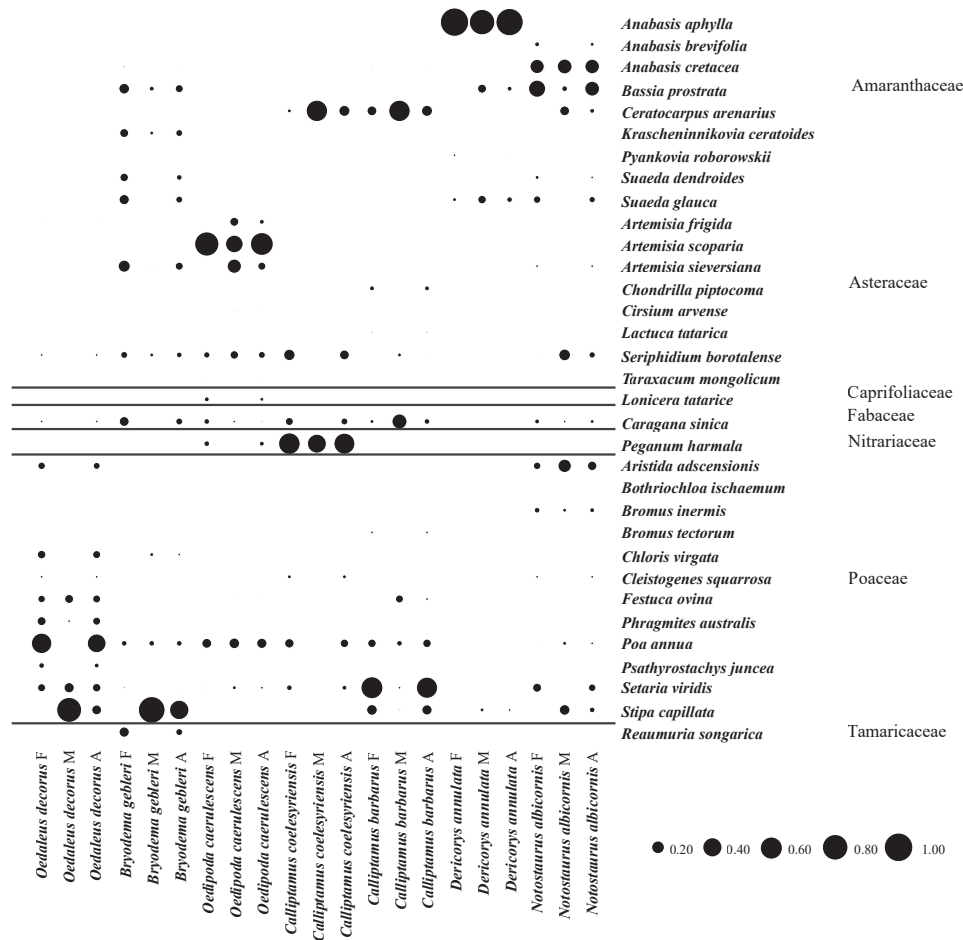


Fig. 3. Relative feeding frequency (RFN) of seven grasshopper species on plants, showing different feeding levels. The absence of circles means that the plants are not eaten. After the grasshoppers' species names, F = female, M = male and A= female+male. The horizontal bars separate distinct taxonomic groups of plants.

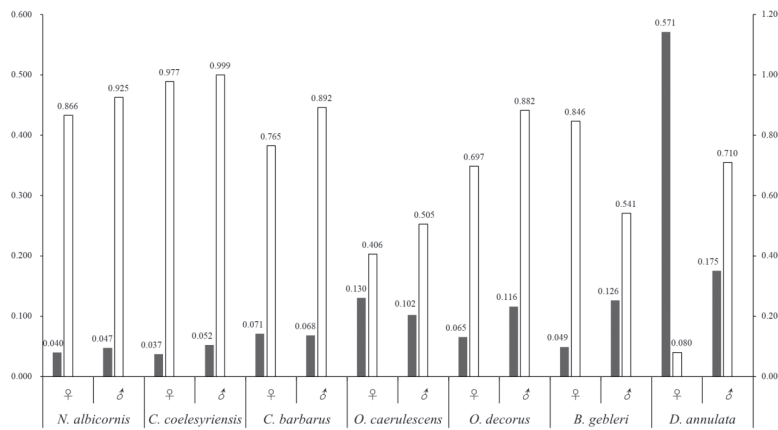


Fig. 4. Differences in individual feeding habits of seven grasshopper species according to Kendall's coefficient of concordance. Note: Kendall values range from 0 to 1; the smaller the value, the greater the variability. P value less than 0.05 represents consistency

were in the range of 0.080–0.999. Individual feeding differences among the three oligophagous grasshoppers (*Oedaleus decorus* males, *Bryodema gebleri* males, and *Dericorys annulata* males and females) are smaller, and their Kendall values ranged from 0.116 to 0.175, which are all larger than those of the four polyphagous grasshoppers (*Oedipoda caerulea*, *Calliptamus barbarus*, *Notostaurus albicornis*, and *Calliptamus colesyi* females). The greatest individual differences among the seven grasshopper species were

found in *Notostaurus albicornis* and *Calliptamus colesyi*, as these two grasshoppers had the smallest Kendall values (which can also be seen as a greater variety of colors in Fig. 5). For example, among females, *Calliptamus colesyi* had the smallest Kendall value of 0.037, and among males, *Notostaurus albicornis* had the smallest Kendall value of 0.047 (Fig. 4). As shown in Fig. 5, there were oligophagous individuals among polyphagous grasshoppers and monophagous individuals among oligophagous grasshoppers.

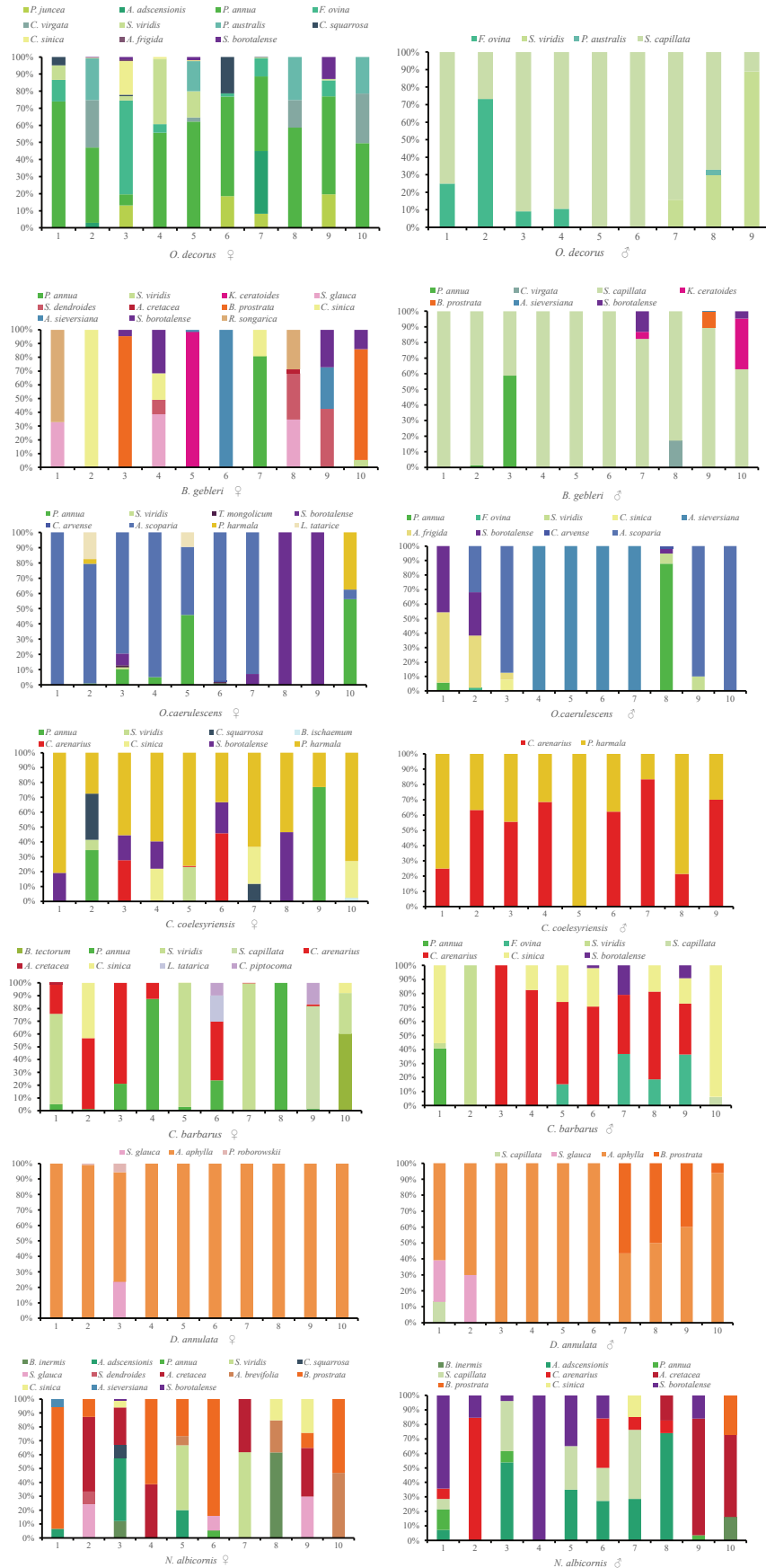


Fig. 5. Interindividual feeding variation in seven grasshopper species (one *Oedaleus decorus* male and one *Calliptamus coelestis* male each had no food in their crop, so only nine are shown feeding).

Table 2. Overlap of the ecological niches of seven grasshopper species by sex.

		<i>O. decorus</i>		<i>B. gebleri</i>		<i>O. caerulescens</i>		<i>C. coelesyriensis</i>		<i>C. barbarus</i>		<i>D. annulata</i>		<i>N. albicornis</i>	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
<i>O. decorus</i>	♀		0.16	0.07	0.07	0.14	0.19	0.18	0.00	0.19	0.14	0.00	0.00	0.18	0.11
	♂			0.00	0.76	0.00	0.02	0.04	0.00	0.26	0.09	0.00	0.02	0.10	0.14
<i>B. gebleri</i>	♀				0.11	0.13	0.29	0.18	0.00	0.07	0.19	0.02	0.19	0.28	0.14
	♂					0.06	0.06	0.06	0.00	0.18	0.06	0.00	0.05	0.03	0.20
<i>O. caerulescens</i>	♀						0.56	0.24	0.04	0.11	0.10	0.00	0.00	0.03	0.08
	♂							0.23	0.00	0.12	0.09	0.00	0.00	0.05	0.12
<i>C. coelesyriensis</i>	♀								0.46	0.17	0.17	0.00	0.00	0.08	0.21
	♂									0.12	0.56	0.00	0.00	0.00	0.12
<i>C. barbarus</i>	♀										0.19	0.00	0.02	0.13	0.29
	♂											0.00	0.00	0.04	0.18
<i>D. annulata</i>	♀												0.80	0.00	0.00
	♂													0.17	0.06
<i>N. albicornis</i>	♀														0.40
	♂														

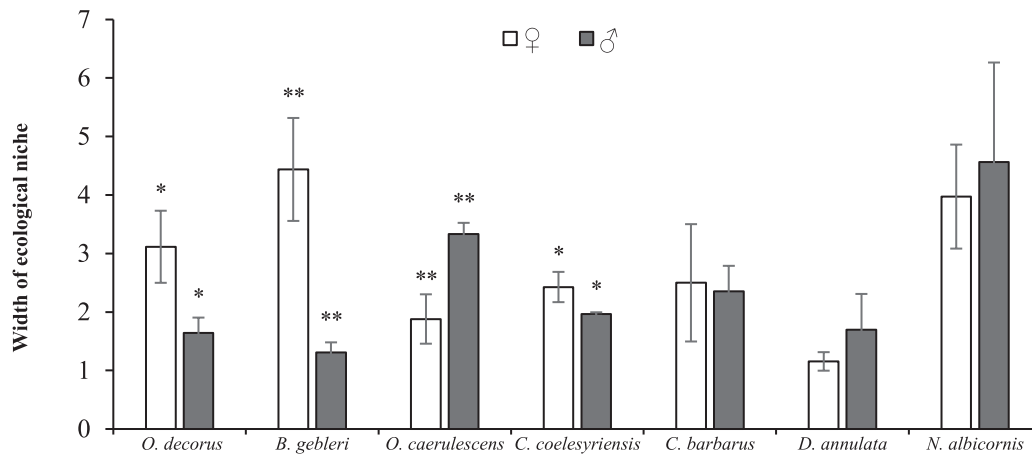


Fig. 6. Ecological niche widths in seven grasshopper species according to sex. Note: t-tests were conducted for each sex in each grasshopper species. One or two asterisks indicate a significant difference at $P < 0.05$ or $P < 0.01$, respectively.

Dietary specialization. Insects exhibit different degrees of specialization in their feeding habits, ranging from monophagy to oligophagy to polyphagy. In this study, it was found that whether *Oedaleus decorus*, *Bryodema gebleri*, and *Calliptamus coelesyriensis* were oligophagous or polyphagous depended on their sex: females showed polyphagous behavior while males showed oligophagous behavior. The rest of the grasshoppers showed the same behavior in males and females; for example, *Dericorys annulata* was oligophagous and *Oedipoda caerulescens*, *Calliptamus barbarus*, and *Notostaurus albicornis* were polyphagous (Fig. 1). Among the oligophagous grasshoppers, male *Oedaleus decorus* (98.11%) and *Bryodema gebleri* (93.12%) consumed primarily Poaceae, whereas *Dericorys annulata* (99.17%) fed primarily on Amaranthaceae (Fig. 2). *Notostaurus albicornis*, one of the polyphagous grasshoppers, had the broadest feeding range, feeding on 15 plant species from four families, whereas *Calliptamus coelesyriensis* had the narrowest range, feeding on only eight species from five families (Fig. 1). The seven grasshopper species in this study consumed a variety of plant families. For example, *Oedaleus decorus*, *Bryodema gebleri*, and *Calliptamus barbarus* consumed mainly Poaceae; *Dericorys annulata* fed primarily on Amaranthaceae; *Notostaurus albicornis* fed on both Poaceae and Amaranthaceae; *Oedipoda caerulescens* fed primarily on Asteraceae; and *Calliptamus coelesyriensis* fed primarily on Nitrariaceae (Figs 2, 3). Among the three grasshopper species that consumed primarily Poaceae, we observed differences in the specific

plant species preferred. For example, we observed high choice for *Oedaleus decorus* feeding on *Poa annua* (RFN = 0.55, as below), *Bryodema gebleri* feeding on *Stipa capillata* (0.55), and *Calliptamus barbarus* feeding on *Setaria viridis* (0.55) (Fig. 3).

Niche analysis.—Sex variation in ecological niches. Next, we performed t-tests to determine the ecological niche widths of male and female grasshoppers across seven locations. Only *Oedaleus decorus*, *Bryodema gebleri*, *Oedipoda caerulescens*, and *Calliptamus coelesyriensis* displayed a notable variance in sexual dimorphism. The feeding ecological niches of female *Oedaleus decorus* and *Calliptamus coelesyriensis* were significantly wider than those of their male counterparts ($P = 0.019$, $0.037 < 0.05$), and for female *Bryodema gebleri*, the niche was highly significantly wider than for their male counterparts ($P = 0.004 < 0.01$), whereas the male feeding ecological niches of *Oedipoda caerulescens* were highly significantly wider than those of the females ($P = 0.006 < 0.01$) (Fig. 6). Most of the overlap of ecological food niches among the seven grasshoppers are not highly differentiated (i.e., there is no significant potential for competition). For example, the ecological niche overlap between the seven grasshopper species ranged from 0 to 0.56, and only the ecological niche overlap between males of *Bryodema gebleri* and males of *Oedaleus decorus* was relatively high ($C_{it} = 0.76 > 0.6$), which may indicate a potential competitive relationship (Table 2).

Comparison of ecological niches. Among the seven grasshopper species, *Notostaurus albicornis* and *Oedaleus decorus* exhibited significantly greater niche widths ($P < 0.05$), measured at 5.22 and 4.02, respectively (Fig. 7). In contrast, *Oedipoda caerulescens* and *Dericorys annulata* had significantly narrower niche widths ($P < 0.05$), measured at 2.49 and 1.22, respectively. Meanwhile, no significant differences were observed ($P > 0.05$) in the niche widths of *Bryodema gebleri*, *Calliptamus barbarus*, and *Calliptamus coelesyriensis*. As can be seen in Table 3, the overlap of ecological food niches among the seven species of grasshoppers was low, with values ranging from 0 to 0.31, indicating that none of the seven species of grasshoppers had any obvious potential competitive relationship with another. The highest food ecological overlap was 0.31 between *Calliptamus barbarus* and *Oedaleus decorus*, and the lowest food ecological overlap, between *Dericorys annulata* and *Oedipoda caerulescens* and *Calliptamus coelesyriensis*, was 0. Overall, *Calliptamus barbarus* had a stronger potential for competition with the other six grasshoppers, and its ecological overlap with the other grasshoppers ranged from 0.10 to 0.31, while *Dericorys annulata* had almost no potential competition with the other six grasshoppers, and its ecological overlap with other grasshoppers was 0.00–0.09.

Discussion

Herein, we present the results of using MACC to examine sex-specific, interindividual, and interspecies differences in dietary patterns in seven grasshopper species present in the Xinjiang grasslands. Previously, it was reported that *Oedaleus decorus* and *Bryodema gebleri* were oligophagous and *Calliptamus coelesyriensis* was polyphagous. In the present study, we found that whether *Oedaleus decorus*, *Bryodema gebleri*, and *Calliptamus coelesyriensis* are oligophagous or polyphagous depends on their sex, such that the females are polyphagous and the males are oligophagous, which has not been reported previously. There were significant sex differences in the feeding habits of the seven grasshoppers, and females displayed a greater tendency to consume more host plant species than males. In addition, adults displayed sex-specific differences in high-preference food sources. Individuals of all seven grasshoppers showed different degrees of dietary variance, with oligophagous grasshoppers (*Oedaleus decorus* males, *Dericorys annulata*, and *Bryodema gebleri* males) showing a smaller degree of individual dietary variance than polyphagous grasshoppers (*Oedipoda caerulescens*, *Calliptamus coelesyriensis* females, *Calliptamus barbarus*, and *Notostaurus albicornis*) and *Calliptamus coelesyriensis* and *Notostaurus albicornis* showing the strongest individual variance in their diets. Oligophagous individuals were present in polyphagous grasshoppers (*Oedaleus decorus* females, *Calliptamus coelesyriensis* females, *Oedipoda caerulescens* females, and *Notostaurus albicornis* females); monophagous individuals were present in oligophagous grasshoppers (*Oedaleus decorus* males, *Bryodema gebleri* males, *Calliptamus coelesyriensis* males, and *Dericorys annulata*).

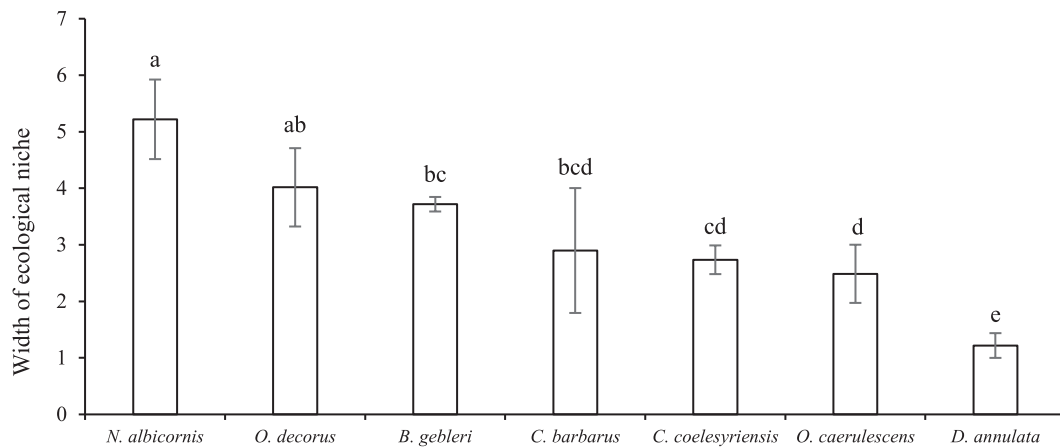
Host plant preference.—In a study on the dietary habits, trophic specialization, and degree of trophic specialization exhibited by 65 species of grasshoppers in the lower Volga River region of Russia, Savitsky (2010) concluded that *Oedaleus decorus*, *Calliptamus coelesyriensis*, and *Notostaurus albicornis* are oligophagous, whereas *Oedipoda caerulescens* and *Calliptamus barbarus* are polyphagous. In this study, we found that the degree of trophic specialization of four species of grasshoppers—*Oedaleus decorus* males, *Calliptamus coelesyriensis* males, *Oedipoda caerulescens*, and *Calliptamus barbarus*—

was consistent with that found in Stavitsky's (2010) study, but the degree of trophic specialization of *Calliptamus coelesyriensis* females and *Notostaurus albicornis* were completely opposite: *Calliptamus coelesyriensis* females and *Notostaurus albicornis* were polyphagous. In Central Asia, *Calliptamus coelesyriensis* feeds on plants belonging to the Asteraceae and Amaranthaceae, such as *Artemisia terrae-albae*, *Artemisia sublessingiana*, wormwoods from the Asteraceae, and perennial saltworts from the Amaranthaceae. *Notostaurus albicornis* feeds on wormwoods (*Artemisia terrae-albae* and *Artemisia sublessingiana*) from the Asteraceae, *Poa bulbosa* and *Carex physodes* from the Poaceae, and *Strigosella africana* from the Brassicaceae (Serkova 1958, 1961, Soyunov 1997). Consequently, we inferred that both *Calliptamus coelesyriensis* and *Notostaurus albicornis* exhibit polyphagous feeding habits that are characteristic of insects that feed on plants across multiple families. Savitsky (2010) narrowly defined these two grasshoppers as oligophagous for selectively feeding on plants from one or two families or on plants from both families in the same habitat. Our results contrast with those of Savitsky owing to differences in the criteria for defining the degree of diet feeding. In addition, our findings revealed that *Notostaurus albicornis* has a more extensive feeding range than previously appreciated: in our study, it fed on 15 plant species from four families, notably Poaceae (*Aristida adscensionis*) and Amaranthaceae (*Anabasis cretacea* and *Bassia prostrata*), many of which have not previously been reported. Although *Dericorys annulata*'s feeding habits have yet to be reported, a comparison with its parent-relative *Dericorys tibialis* (Pallas 1773) indicated identical feeding habits; for example, *Dericorys tibialis* feeds primarily on *Anabasis aphylla* of the Amaranthaceae but also feeds on *Salsola verrucosa*, *Petrosimonia brachiata*, and *Suaeda* sp. (Li and Xia 2006, Savitsky 2010). We found that none of the seven species of grasshoppers primarily selected plants that were dominant in their habitats and that their feeding on plants did not depend exclusively on the relative abundance of plants in their habitats, which is indirect evidence that grasshoppers are actively selecting food.

Grasshoppers more closely related often exhibit more similar feeding habits (Savitsky 2010). Huang (1995) observed that grasshoppers from the subfamily Catantopinae feed primarily on dicotyledons, whereas some species from the subfamily Oedipodinae consume both dicotyledons and monocotyledons. Within the Calliptaminae and Dericorythidae, *Calliptamus barbarus*, *Calliptamus coelesyriensis*, and *Dericorys annulata* demonstrate varying choices for plant types (dicotyledons and monocotyledons). Specifically, *Calliptamus coelesyriensis* and *Dericorys annulata* feed primarily on dicotyledons: *Calliptamus coelesyriensis* consumes mainly Nitrariaceae, whereas *Dericorys annulata* consumes mainly Amaranthaceae. The exception to this pattern is *Calliptamus barbarus*, which feeds predominantly on monocotyledons (Poaceae). This finding may be attributable to differences in sex and geographic location. Our research indicates that *Calliptamus barbarus* females consumed primarily monocotyledons from the Poaceae, whereas males tended to feed on dicotyledons from the Amaranthaceae and Nitrariaceae. In Central Asia, the insect feeds mostly on dicotyledonous plants (Lehr 1962, Stoliarov 1979, Soyunov 1997), whereas in Russia it feeds on both dicotyledonous and monocotyledonous plants (Chernyakhovskii 1968). At different sites, the feeding choices of *Calliptamus barbarus* were consistent at the plant family level and varied at the species level, which may be related to different feeding strategies in different habitats. Differences in vegetation composition among habitats and differences in nutrient content of the same species in different habitats affect grasshoppers' feeding choices (Meriem et al. 2021, Pitteloud et al. 2021, König et al. 2022).

Table 3. Overlap in the food ecological niches of seven grasshopper species.

	<i>O. decorus</i>	<i>B. gebleri</i>	<i>O. caerulescens</i>	<i>C. coelesyriensis</i>	<i>C. barbarus</i>	<i>D. annulata</i>	<i>N. albicornis</i>
<i>O. decorus</i>		0.19	0.15	0.14	0.31	0.01	0.21
<i>B. gebleri</i>			0.16	0.22	0.21	0.09	0.26
<i>O. caerulescens</i>				0.19	0.10	0.00	0.08
<i>C. coelesyriensis</i>					0.30	0.00	0.15
<i>C. barbarus</i>						0.01	0.18
<i>D. annulata</i>							0.09
<i>N. albicornis</i>	0						0.31

**Fig. 7.** Ecological niche widths for seven grasshopper species. Note: Data are shown as mean \pm SD. Different letters indicate significant differences ($P < 0.05$), according to Duncan's new multiple range method.

Our findings, combined with previous findings on grasshopper feeding patterns, indicate that *Oedaleus decorus* exhibits a high-preference feeding on Poaceae (*Poa annua*) (Huang 1995, Wang 2007), *Calliptamus barbarus* has high-preference feeding on Poaceae (Savitsky 2010), whereas *Oedipoda caerulescens* shows high-preference feeding on Asteraceae (wormwoods) (Savitsky 2010) and was shown to feed on many families, including Asteraceae, Apiaceae, Rosaceae, Fabaceae, Caryophyllaceae, Crassulaceae, Brassicaceae, Poaceae, and Lamiaceae in Europe (Meriem et al. 2021, Pitteloud et al. 2021, König et al. 2022). Moreover, the high-preference feeding habits of *Calliptamus coelesyriensis* and *Bryodema gebleri* differ significantly. For example, *Calliptamus coelesyriensis* has been shown high-preference feeding on Asteraceae (Wang 2007, Savitsky 2010), whereas the present study indicates high-preference feeding on Nitrariaceae (*Peganum harmala*). Similarly, *Bryodema gebleri* has been shown high-preference feeding on Boraginaceae (Huang 1995); however, we observed high-preference feeding on Poaceae (*Stipa capillata*). We suggest three possible causes for these differences. The first potential cause may be differences in research methods: Wang (2007) and Huang (1995) both used the caging method, which entails passive and non-selective feeding of grasshoppers, but the present study used the MACC method, which involves naturally selective feeding. The second possibility is differences in feeding habits across geographical locations: Huang's study was conducted in Balikun, which is in Xinjiang's Hami region, whereas our research was conducted in Bole in the Bozhou region of Xinjiang. Plant composition/species at each sampling site may have a strong influence on the selection of host plants by orthopteran insects (Meriem et al. 2021, Pitteloud et al. 2021, König et al. 2022). The third possibility is that *Calliptamus coelesyriensis* may feed on *Peganum harmala* for hydration purposes: grasshoppers tend to feed on water-rich plants during the dry season to replenish their fluids (Ohabuikie 2009).

We observed significant differences in the feeding habits of the sexes. We speculate that these differences might be attributable to the heavier body weight of female grasshoppers as well as their choice for laying eggs on the ground, thus resulting in the tendency of adult females to move along the lower parts of plants or on the ground surface more frequently than males (Yan and Chen 1997). The differences in feeding range and plant preference were reflected in the sex-specific of the three grasshopper species studied. Specifically, females consumed more host plant species than males, and adult males and females had different high-preference feeding plants. These findings are consistent with those of previous studies; for example, females of *Cornops aquaticum* have a wider feeding range, feeding on six species of plants, while males feed on five species of plants (Capello et al. 2011). Female *Romalea microptera* tend to feed on *Spartina alterniflora* (Poaceae), whereas males prefer *Sesbania macrocarpa* (Fabaceae) (Vincent 2006); *Oedaleus decorus* females exhibit a preference for *Leymus chinensis* over *Artemisia frigida*, whereas males prefer *Artemisia frigida* over *Leymus chinensis* (Qin 2016); females of *Ageneotettix deorum* and *Phoetaliotes nebrascensis* have a greater preference for proline-rich food sources (Behmer and Joern 1994); and male *Oedaleus senegalensis* show a preference for host leaves while females prefer host maize ears (Boys 1978). These feeding choices may reflect adaptations to physiological needs, as males require high-fat foods for flight and females require high-protein foods for ovarian development (Schoonhoven et al. 2005). Thus, female grasshoppers must consume adequate nutrition to support their reproductive activity, particularly ovarian growth, potentially accounting for the observed differences in feeding habits between the sexes (Behmer and Joern 1994). Furthermore, females may require greater food intake than males to fuel their metabolic needs owing to their larger size (Ueckert and Hansen 1971).

Considerable interindividual variation in feeding on host plants exists among insects (Schoonhoven et al. 2005). Many authors argue that individuals are often specialized and that population-level polyphagy in many insect species is a result of specialization on many different resources by individuals within the population (Singer 1983, Via 1984, Halima et al. 1985, Braker 1987, Howard et al. 1994). Our experimental results are not consistent with this view: among polyphagous grasshopper species, most individuals are also polyphagous, and only a small number of oligophagous individuals exist. For example, among the seven species, *Oedaleus decorus* had the most oligophagous individuals, accounting for 50%, and the remaining polyphagous grasshoppers had oligophagous individuals in the range of 0–30%. In this study, it was found that all seven species of grasshopper had different degrees of individual feeding differences, and the degree of individual feeding differences was related to the feeding range, with three species of oligophagous grasshoppers—*Oedaleus decorus* males, *Dericorys annulate*, and *Bryodema gebleri* males—having fewer individual feeding differences, and five species of polyphagous grasshoppers—*Oedipoda caerulescens*, *Calliptamus coelesyriensis*, *Calliptamus barbarus*, *Notostaurus albicornis*, and *Bryodema gebleri* females—having more differences. *Calliptamus coelesyriensis* and *Notostaurus albicornis* exhibited greater differences than the others, which is consistent with our hypothesis. According to Howard (1995), *Melanoplus differentialis* and *Schistocerca albolineata*, which are polyphagous grasshoppers, exhibit variations in interindividual plant choice, degree of choice, and food range. Howard (1995) also found that environmental heterogeneity is primarily responsible for these interindividual feeding variations, although the order of encounters, supplemental resource consumption, and intrinsic feeding traits are also influencing factors (Howard 1995). The reasons and mechanisms underlying the variability in dietary choice among these five omnivorous grasshopper species have not yet been established. Interindividual variation resulting from genetic polymorphisms, developmental plasticity, and elevated interindividual phenotypic and genetic variation can promote the ecological and evolutionary success of populations and species amid environmental change (Forsman and Wennersten 2016). More variable populations are less susceptible to environmental fluctuations, exhibit lower population size fluctuation, have higher establishment success rates and larger distribution ranges, and are less prone to extinction (Forsman and Wennersten 2016). Therefore, *Calliptamus coelesyriensis* and *Notostaurus albicornis*, the most environmentally adapted among the seven grasshopper species investigated, may serve as valuable experimental models for investigating the relationship between interindividual variations and environmental adaptation.

The feeding habits of grasshoppers are related to the insect's body (the grasshopper itself) and the plant. Where genetic variation in the insect body itself determines its feeding choices (Howard 1993), grasshoppers have well-defined nutritional requirements in terms of carbohydrate, protein, and water intake (Simpson et al. 2004). As a result, they develop the cognitive ability to taste and learn how to select foods accurately (Bernays and Bright 2005). They show distinct preference for foods containing different nutrients (Behmer and Joern 2008), and feeding on these appropriate foods improves grasshopper adaptation (Simpson et al. 2004), allowing them to survive and reproduce successfully. The influences of plants are manifested in physical characteristics, chemical characteristics, and phylogenetic relationships, whereas physical characteristics are manifested in leaf toughness and leaf epidermal hairs; the toughness of plant leaves can limit grasshopper feeding, nutrient uptake, and, ultimately, growth (Ibanez et al. 2013b). For example, unidirectional

epidermal leaf hairs guide small herbivores away from the plant's meristematic tissues so that valuable parts of the plant are less damaged (Karban et al. 2019). In addition, the chemical characteristics of plants contain nutrients and secondary compounds that vary from plant to plant, and grasshoppers feed selectively in order to balance nutrients and reduce the intake of secondary compounds (Rappaport 1980, Nik et al. 2021). Thus, plant phylogeny interacts with other factors to shape the specialization of herbivore communities (König et al. 2022), which influences grasshopper feeding.

Grasshopper feeding choice is a complex behavior composed of many factors, and this study provides a view of the feeding status of only seven grasshopper species in a particular habitat and environment under natural conditions, rather than demonstrating intrinsic differences in the plant-food preference of species. Therefore, future studies should examine the feeding of grasshoppers in different habitats and at different altitudes and latitudes in order to analyze intrinsic feeding patterns of host-plant use of grasshoppers. To accurately characterize the diet of Orthoptera, a large number of individuals and interspecies must be analyzed, and it is necessary to pay attention to the obvious differences in plant consumption between males and females.

Potential intraspecific and interspecific competition.—Two grasshopper species that come from the same locations and have similar feeding tendencies may engage in intense competition (Liu et al. 2007). In this study, we observed that interspecific competition among grasshoppers correlated with sex. Specifically, four species of grasshopper (*Bryodema gebleri*, *Oedaleus decorus*, *Calliptamus coelesyriensis*, and *Calliptamus barbarus*) showed greater ecological niche overlap among males than any other group of species, suggesting that these four species have the most similar host plant composition. *Calliptamus barbarus* exhibited strong interspecific competition with *Oedaleus decorus* and *Calliptamus coelesyriensis*, and these three species often coexist in the same habitat. Liu et al. (2007) examined three grasshopper species in Gansu and determined that intraspecific competition is restricted primarily by nutritional inadequacy, whereas interspecific competition is influenced mainly by environmental conditions and grasshoppers' adaptation to these conditions (Liu et al. 2007). The present study constitutes a preliminary analysis of the ecological niches of grasshoppers and reveals potential competitive associations. In future research, we plan to perform deeper investigations into the symbiotic conditions of grasshoppers, including sex, density, and food, to account for their competitive relationships.

Contributions

LZ and JLR designed the experiments. WJK and KXL performed the experiments. WJK and JLR analyzed the data. JXL and XJ provided technical and material support. LZ, JLR, and WJK wrote the manuscript. All authors reviewed and considered the manuscript.

Competing financial interests

The authors declare no competing financial interests.

Acknowledgments

This research was supported by the Special Fund for Grassland Ecological Restoration Project in Bortala Mongol Autonomous Prefecture, P.R. China, and National Science and Technology Basic Resources Survey (2019FY100403).

References

- Behmer ST, Joern A (1994) The influence of proline on diet selection: sex-specific feeding preferences by the grasshoppers *Ageneotettix deorum* and *Phoetaliotes nebrascensis* (Orthoptera: Acrididae). *Oecologia* 98: 76–82. <https://doi.org/10.1007/BF00326093>
- Behmer ST, Joern A (2008) Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* 105: 1977–1982. <https://doi.org/10.1073/pnas.0711870105>
- Bernays E, Bright K (2005) Distinctive flavours improve foraging efficiency in the polyphagous grasshopper, *Taeniopoda eques*. *Animal behaviour* 69: 463–469. <https://doi.org/10.1016/j.anbehav.2004.04.020>
- Boys H (1978) Food selection by *Oedaleus senegalensis* (Acrididae: Orthoptera) in grassland and millet fields. *Entomologia Experimentalis et Applicata* 24: 278–286. <https://doi.org/10.1111/j.1570-7458.1978.tb02783.x>
- Braker H (1987) Host plant relationships of the neotropical grasshopper, *Microtylopteryx hebaridi* Rehn (Acrididae: Ommatolampinae) (feeding ecology, Costa Rica) PhD thesis, City of Berkeley: University of California, Berkeley.
- Capello S, De Wysiecki ML, Marchese M (2011) Feeding patterns of the aquatic grasshopper *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae) in the middle Paraná River, Argentina. *Neotropical Entomology* 40: 170–175.
- Chen YL (1981) Studies on the Acridoids of Xinjiang Uighur Autonomous region-distribution of Acridoids. 1. faunal and regional distribution. *Acta Entomologica Sinica* 24: 17–27.
- Chernyakhovskii ME (1968) Feeding types and mandible structure in different life forms of grasshoppers (Acridoidea). *Zoologicheskii zhurnal* 47: 238–248.
- Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. *Ecology* 52: 567–576. <https://doi.org/10.2307/1934144>
- Costa OG (1836) *Fauna del regno di Napoli*. Ortotteri.
- ElEla SA, ElSayed W, Nakamura K (2010) Mandibular structure, gut contents analysis and feeding group of orthopteran species collected from different habitats of Satoyama area within Kanazawa City, Japan. *Journal of Threatened Taxa* 2: 849–857. <https://doi.org/10.11609/JoTT.o2346.849-57>
- Eversmann EV (1848) *Additamenta quaedam levia ad Fischeri de Waldheim Orthoptera Rossica*, 15 pp.
- Fieber FX (1853) *Synopsis der europäischen Orthoptera mit besonderer Rücksicht auf die in Böhmen vorkommenden Arten*. Lotos, Zeitschrift für Naturwissenschaften. Herausgegeben vom naturhistorischen Vereine Lotos in Prag.
- Fischer VW (1836) *Orthoptera duo e montibus Catunicis descripta et icone illustrata*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 9: 346–349.
- Forsman A, Wennersten L (2016) Inter-individual variation promotes ecological success of populations and species: Evidence from experimental and comparative studies. *Ecography* 39: 630–648. <https://doi.org/10.1111/ecog.01357>
- Fry B, Joern A, Parker PL (1978) Grasshopper food web analysis: Use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. *Ecology* 59: 498–506. <https://doi.org/10.2307/1936580>
- Gall P L, Djihou Z, Tchenga G, Lomer CJ (2003) Diet of *Zonocerus variegatus* (Linné, 1758) (Orthoptera, Acrididae) in cassava fields in Benin. *Journal of Applied Entomology* 127: 435–440. <https://doi.org/10.1046/j.1439-0418.2003.00762.x>
- Germar (1824) *Insectorum species novae aut minuscognitae descriptionibus illustratae*. <https://doi.org/10.5962/bhl.title.130964>
- Giglio-Tos E (1893) *Viaggio del Dr. E. Festa in Palestina, nel Libano e regioni vicine*. V. Ortotteri. *Bollettino dei Musei di Zoologia ed Anatomia comparata della Royal Università di Torino* 8, 1–18. <https://doi.org/10.5962/bhl.part.27226>
- Halima TB, Gillon Y, Louveaux A (1985) Spécialisation trophique individuelle dans une population de *Dociostaurus maroccanus* (Orthopt: Acrididae). *Acta oecologica Oecologia generalis* 6: 17–24.
- Howard JJ (1993) Temporal pattern of resource use and variation in diets of individual grasshoppers (Orthoptera: Acrididae). *Journal of Insect Behavior* 6: 441–453. <https://doi.org/10.1007/BF01049524>
- Howard JJ (1995) Variation in dietary patterns among and within polyphagous grasshopper species (Orthoptera: Acrididae). *Journal of Insect Behavior* 8: 563–577. <https://doi.org/10.1007/BF01997231>
- Howard JJ, Raubenheimer D, Bernays EA (1994) Population and individual polyphagy in the grasshopper *Taeniopoda eques* during natural foraging. *Entomologia Experimentalis et Applicata* 71: 167–176. <https://doi.org/10.1111/j.1570-7458.1994.tb01782.x>
- Huang CM (1995) A study on the relationship between the feeding habits of the dominant species of locusts and the taxonomic system of the middle subfamily of Acrididae in Balikun Grassland, Xinjiang. *Entomotaxonomia* 17: 128–134.
- Ibanez S, Manneville O, Miquel C, Taberlet P, Valentini A, Aubert S, Coisac E, Colace MP, Duparc Q, Lavorel S, Moretti M (2013a) Plant functional traits reveal the relative contribution of habitat and food preferences to the diet of grasshoppers. *Oecologia* 173: 1459–1470. <https://doi.org/10.1007/s00442-013-2738-0>
- Ibanez S, Lavorel S, Puijalon S, Moretti M (2013b) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Functional Ecology* 27: 479–489. <https://doi.org/10.1111/1365-2435.12058>
- Joern A (1983) Host plant utilization by grasshoppers (Orthoptera Acrididae) from a Sandhills Prairie. *Journal of Range Management* 36: 793–797. <https://doi.org/10.2307/3898212>
- Joern A (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): Factors influencing diet specialization. *Oecologia* 38: 325–347. <https://doi.org/10.1007/BF00345192>
- Kang L, Chen YL (1994a) Multidimensional analysis of resource utilization in assemblages of rangeland grasshoppers (Orthoptera Acrididae). *Insect Science* 1: 264–282. <https://doi.org/10.1111/j.1744-7917.1994.tb00253.x>
- Kang L, Chen YL (1994b) in Inner Mongolia. *Acta Entomologica Sinica* 37: 178–189.
- Kang L, Han X, Zhang Z, Sun OJ (2007) Grassland ecosystems in China: review of current knowledge and research advancement. *Philosophical transactions of the royal society B: Biological Sciences* 362: 997–1008. <https://doi.org/10.1098/rstb.2007.2029>
- Karban R, LoPresti E, Vermeij GJ, Latta R (2019) Unidirectional grass hairs usher insects away from meristems. *Oecologia* 189: 711–718. <https://doi.org/10.1007/s00442-019-04355-7>
- König S, Krauss J, Keller A, Bofinger L, Steffan-Dewenter I (2022) Phylogenetic relatedness of food plants reveals highest insect herbivore specialization at intermediate temperatures along a broad climatic gradient. *Global Change Biology* 28: 4027–4040. <https://doi.org/10.1111/gcb.16199>
- Lan B, Dong Y, Niklas KJ, Sun S (2021) Dietary differences between grasshoppers are associated with life history tradeoffs in an alpine meadow. *Ecological Research* 36: 842–853. <https://doi.org/10.1111/1440-1703.12248>
- Ler AP (1962) Materials on the biology of the Turanian and desert pruce (Orthoptera, Calliptamus) in the Chimkent region. *Zashchita Rasteni* 7: 3–56. [in Russian]
- Levins R (1968). *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, 55 pp. <https://doi.org/10.1515/9780691209418>
- Li HC, Xi RH, Chen YL (1983) Feeding characteristics of typical grassland locusts in Inner Mongolia 1. Feeding characteristics under cage feeding. *Acta Entomologica Sinica* 3: 214–228.
- Li HC, Xia KL (2006) *Fauna Sinica, Insecta, Vol. 43, Orthoptera, Acridoidea, Catantopidae*. Science Press, Beijing, 576 pp.
- Li YK, Chen ZA, Gong Y, Chen XJ (2021) A review on the methods used in trophic niche studies of marine animals and their applications. *Journal of Tropical Oceanography* 40: 143–156.
- Linnaeus C (1758) *In Systema Naturae per Regna tria naturae* (10th ed.). Holmiae. Vol. 1, 824 pp.

- Liu C, Zhou S, Yan L, Huang F (2007) Competition among the adults of three grasshoppers (Orthop., Acrididae) on an alpine grassland. *Journal of Applied Entomology* 131: 153–159. <https://doi.org/10.1111/j.1439-0418.2006.01114.x>
- Maklakov AA, Simpson SJ, Zajitschek E, Hall MD, Dessmann J, Clissold F, Raubenheimer D, Bonduriansky R, Brooks RC (2008) Sex-specific fitness effects of nutrient intake on reproduction and lifespan. *Current Biology* 18: 1062–1066. <https://doi.org/10.1016/j.cub.2008.06.059>
- McClenaghan B, Gibson JF, Shokralla S, Hajibabaei M (2015) Discrimination of grasshopper (Orthoptera: Acrididae) diet and niche overlap using next - generation sequencing of gut contents. *Ecology and Evolution* 5: 3046–3055. <https://doi.org/10.1002/ece3.1585>
- Meriem D, Lotfi M, Nadhira B (2021) Diet of *Oedipoda miniata mauritania* and *Oedipoda coerulescens sulfurescens* (Orthoptera: Acrididae) on the coast of the Tlemcen region (Algeria). *Ukrainian Journal of Ecology* 11: 21–27.
- Muhetaer, Ayiding, Gulizhaer (2000) Present situation and prospect of pastoral animal husbandry in Xinjiang. *Pratacultural Science* 17: 79–82.
- Nan ZB (2022) Remote sensing application to grassland monitoring. Da Silva SC (Ed.) *International Grassland Congress Proceedings. The XIX International Grassland Congress, São Pedro, São Paulo (Brazil), February 2001*. Fundacao de Estudos Agrarios Luiz de Queiroz Publishers, São Paulo – Brazil.
- Ng SH, Simpson SJ, Simmons LW (2019) Sex differences in nutrient intake can reduce the potential for sexual conflict over fitness maximization by female and male crickets. *Journal of Evolutionary Biology* 32: 1106–1116. <https://doi.org/10.1111/jeb.13513>
- Nik N, Putra NS, Martono E (2021) Life table of the migratory locust (*Locusta migratoria* L.) on different host plants. In: *Proceeding the first international conference on government education management and tourism*, 719–729.
- Ohabuikie JE (2009) Grass availability and food preference of the african migratory locust, *Locusta migratoria migratorioides* (R. & F.). *Journal of Applied Entomology* 88: 354–363. <https://doi.org/10.1111/j.1439-0418.1979.tb02513.x>
- Pallas PS (1773) In *Reise durch verschiedene Provinzen des Russischen Reiches*. Kaiserliche Akademie der Wissenschaften, St. Petersburg. Vol. 2, 744 pp.
- Pitteloud C, Walser JC, Descombes P, Novaes de Santana C, Rasmann S, Pellissier L (2021) The structure of plant–herbivore interaction networks varies along elevational gradients in the European Alps. *Journal of Biogeography* 48: 465–476. <https://doi.org/10.1111/jbi.14014>
- Qin XH (2016) Study on the adaptation of *Oedaleus asiaticus* to typical steppe habitats in Inner Mongolia. *Chinese Academy of Agricultural Sciences*, Beijing.
- Rapport DJ (1980) Optimal foraging for complementary resources. *The American Naturalist* 116: 324–346. <https://doi.org/10.1086/283631>
- Savitsky VY (2010) Trophic relationships and their importance for biotopic distribution of grasshoppers (Orthoptera, Acridoidea) in semi-deserts and deserts of the lower Volga river area. *Entomological Review* 90: 830–856. <https://doi.org/10.1134/S0013873810070031>
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408–418. <https://doi.org/10.2307/1935376>
- Schoonhoven LM, Van Loon JJ, Dicke M (2005) *Insect-plant biology*. Oxford University Press, London, Oxford, 211, 216. <https://doi.org/10.1093/oso/9780198525943.001.0001>
- Serkova L (1958) Insect pests of grass stands in Betpak-Dala Pastures. *Zashchita Rastenii* 4: 104–129. [in Russian]
- Serkova L (1961) On the biology of Acrididae and their significance as pests in summer pastures of Sary-Arkin Steppe. *Zashchita Rastenii* 6: 147–157. [in Russian]
- Simpson SJ, Sibly RM, Lee KP, Behmer ST, Raubenheimer D (2004) Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68: 1299–1311. <https://doi.org/10.1016/j.anbehav.2004.03.003>
- Singer MC (1983) Determinants of multiple host use by a phytophagous insect population. *Evolution* 37: 389–403. <https://doi.org/10.2307/2408346>
- Soyunov OS (1997) Significance and trophic specificity of Orthopteroid insects in desert ecosystems (Northern Kara Kum). *Siberian Journal of Ecology* 3: 269–273.
- Stolyarov MV (1979) Dynamics of phytomass consumption by Orthoptera communities of the Iori Plateau in Transcaucasia. *Entomologicheskoe Obozrenie* 58: 42–52.
- Tyrkus M, Gangwere S (1970) Studies on the feculae of selected Michigan Acrididae (Orthoptera). *Michigan Entomologist* 3: 118–128. <https://doi.org/10.22543/0090-0222.1130>
- Ueckert D, Hansen R (1971) Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. *Oecologia* 8: 276–295. <https://doi.org/10.1007/BF00346475>
- Unsicker SB, Oswald A, Köhler G, Weisser WW (2008) Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia* 156: 313–324. <https://doi.org/10.1007/s00442-008-0973-6>
- Via S (1984) The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution* 38: 896–905. <https://doi.org/10.2307/2408399>
- Vincent SE (2006) Sex-based divergence in head shape and diet in the Eastern lubber grasshopper (*Romalea microptera*). *Zoology* 109: 331–338. <https://doi.org/10.1016/j.zool.2006.04.004>
- Wang SG, Ma XM (2009) Food selection and food niche of locust *Catantops pinguis* from Hangzhou, Zhejiang. *Plant Protection* 35: 39–44.
- Wang T (2007) Studies on the choice of seven primary grasshoppers for host plant and system evolution relationships of them in Xinjiang Master: Xinjiang Normal University.
- WRI (1986) *World Resources-A Report by the World Resources Institute and the International Institute for Environment and Development*. Basic Books Inc, New York.
- Yan ZC, Chen YL (1997) Studies on the individual size group and the life form of grasshoppers in typical steppe of inner mongolia, China. *Acta Entomologica Sinica* 17: 666–670.
- Zhang L (2011) Advances and prospects of strategies and tactics of locust and grasshopper management. *Chinese Bulletin of Entomology* 48: 804–810.
- Zhang L, Ban LP, You YW, Yin XW (2020) Locust outbreak and management. *Journal of Environmental Entomology* 42: 511–519.