

*Full Length Research Paper*

# A comparison of species richness of the true bugs (Hemiptera: Heteroptera) among four desert types in Kazakhstan

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**Kazakh insect fauna and biodiversity, especially in arid regions, are largely unknown. We identified species rich (252 species) Heteroptera assemblages associated with four desert types: sandy, solonchak (salt), clay and stony desert. The sandy desert was most species rich (153), followed by the solonchak desert (101), and clay desert (73). The stony desert was the poorest species (61). We found significant differences ( $P=0.05$ ) in Jaccard similarity between pairs of Heteroptera assemblages among all four desert types. However, excluding ubiquitous generalist species, sandy desert Heteroptera assemblages were statistically similar ( $p=0.05$ ) to both the clay desert and to solonchak desert assemblages. Species limited to only one desert type (habitat specialists) were the most common but were unevenly distributed: sandy and solonchak deserts had the highest proportion of habitat specialist species (50 and 54%), while the clay and stony deserts had the lowest (32 and 33%). There were relatively few habitat generalist species (38), but they were nearly half of the Heteroptera of the species-poor stony and clay deserts. Soil characteristics (permeability and texture), and vegetation diversity, abundance and structure may be responsible for the patterns of Heteroptera species distribution among the desert types. The presence of a species rich assemblage of Heteroptera, with a large proportion of habitat specialized species, suggests that Kazakh deserts may support high levels of arthropod diversity and endemism, potentially useful as an indicator for total insect diversity.**

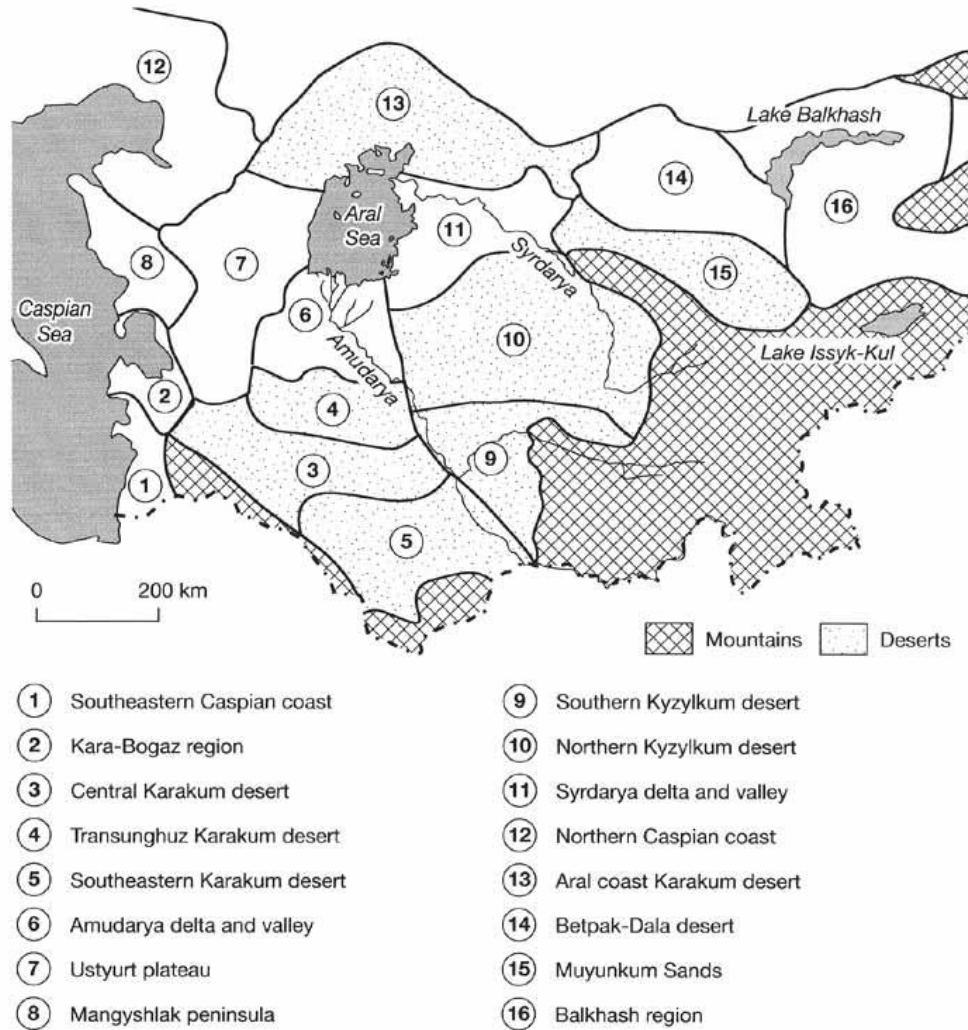
**Key words:** Kazakhstan, Heteroptera, insect conservation, diversity, sandy desert, clay desert, salt desert, stony desert.

## INTRODUCTION

The recognition of species richness and diversity patterns is important because they are fundamental to science-based conservation biology (Leather et al., 2008). A key area of research in insect ecology seeks to identify and explain geographic patterns of species richness. However, much insect ecology remains unknown,

particularly in developing countries and in difficult terrain (Paknia and Pfeiffer, 2011). Large-scale studies of insect biodiversity are scarce, especially outside North America, Australia and Africa, and for deserts, they are even scarcer (Tigar and Osborne, 1997), and so patterns of diversity in many insect taxa in extensive regions and habitats have never been studied. Arid and semi-arid regions of the Palearctic in general, and the mountain, steppe and desert regions of Central Asia in particular, are examples of regions where diversity patterns among insects remains poorly studied (Konstantinov et al.,

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**Figure 1a.** Desert ecoregions of Kazakhstan and the surrounding region (from Lioubimsteva 2002).

2009; Paknia and Pfeiffer, 2011).

The focus of our research was on desert regions because insect biodiversity is known to be high in Palearctic desert areas, with a large percentage of endemic taxa (Konstantinov et al., 2009). Palearctic deserts stretch from Northern Africa to Northwestern China and Western India. Depending on the climatic conditions, soil composition, and vegetation, Palearctic deserts are further divided into three large sub regions: Saharo-Arabian, Irano-Turanian, and Central Asian (Konstantinov et al., 2009). About 124.6 million hectares of Kazakhstan are classified as desert (Figure 1a), subdivided into three climate-related ecoregion types; the Northern, Middle and South desert ecoregions

(Lioubimsteva, 2002; MNRPE, 2009; UNDP, 2005). These correspond to Central Asian northern desert, Kazakh semi-desert and Central Asian southern desert/Caspian lowland desert of the World Wildlife Fund classification (World Wildlife Fund, 2011).

A recent summary (MNRPE, 2009) found that while the inventory of the invertebrate fauna of the country is far from complete, an estimated 80,000+ invertebrate species, including at least 60,000 species of insects, inhabit Kazakhstan. Invertebrate endemism in the country is high, especially in arid regions and mountains, with 85 insect species listed as vulnerable in the Kazakhstan Red Data Book (Chemonics International, 2001). The desert area is the least well known with a

relatively low number of insect species reported (2448) (MNRPE, 2009). Further, only about 100 out of 550 families of insects represented in the fauna of Kazakhstan have been adequately studied and no more than 40% of the species thought to be from Kazakhstan have been found there (MNRPE, 2009). Knowledge of biological and ecological characteristics of known species and their distribution are very poor.

Kazakhstan's desert regions appear to support diverse Heteroptera assemblages. Of the over 1000 species reported to occur in Kazakhstan (Asanova, 1986; Aukema and Rieger, 1995-2006), a large number (879) are found there (MNRPE, 2009). The "true bugs", Heteroptera, of Kazakhstan are a diverse group about which much still remains unknown, even after over 150 years of research. The recognized number of reported Heteroptera species from Kazakhstan exceeds 1000, from 32 families (Asanova, 1986; Aukema and Rieger, 1995-2006). Species richness is comparable with other well studied territories of the Palearctic Region like Mongolia and the Asian and the southern European parts of Russia. As a group, Heteroptera are recognized as an indicator group for total insect diversity, because they are ecologically more diverse and their numbers correlate well with total insect diversity (Ullrich, 2001). Information on the distribution of Heteroptera among desert habitats can inform national biodiversity conservation priorities for these fragile lands.

Threats to Kazakh desert ecosystems are growing, from urbanization, road building, over grazing, conversion of land to agriculture, irrigation and drainage, and oil and gas development (MNRPE, 1999), but national biodiversity assessments and conservation efforts have been limited in the arid regions.

This study is part of an on-going national inventory of invertebrates, a priority recommendation of the Republic of Kazakhstan National Strategy and Action Plan on Conservation and Sustainable Use of Biological Diversity (MNRPE, 2009). The inventory is providing the information needed to develop effective national biodiversity conservation plans (MNRPE, 1999, 2009).

This research was to determine if the various recognized desert types in Kazakhstan supported similar or significantly different Heteroptera species assemblages. The results would provide an indication of the invertebrate diversity values of the different desert types and help decision makers and planners set conservation priorities for large regions of Kazakhstan.

Research on the Heteroptera of the region has been concerned primarily with taxonomy and distribution records (e.g. Asanova, 1986; Golub, 1989; Kerzhner, 1997; Vinokurov et al., 1988;), with some additional work in natural history, including habitat and plant associations e.g. Vinokurov, 2010) and faunal associations.

(Clarifying the taxonomy, species distribution and plant associations lays the groundwork for biodiversity assessments but these data alone are insufficient to guide conservation planning. To establish biodiversity baselines, develop indicators, assess habitat value or measure habitat change requires a systematic and quantitative measurement of relative species richness values, degrees of overlap in species distributions, levels of endemism and association with specific habitat types. This study builds on this previous body of entomological research to improve the understanding of the biodiversity of the region. We use descriptive statistical tools to assess and compare species richness, diversity, endemism and overlaps among the Heteroptera of the desert regions of Kazakhstan.

## MATERIALS AND METHODS

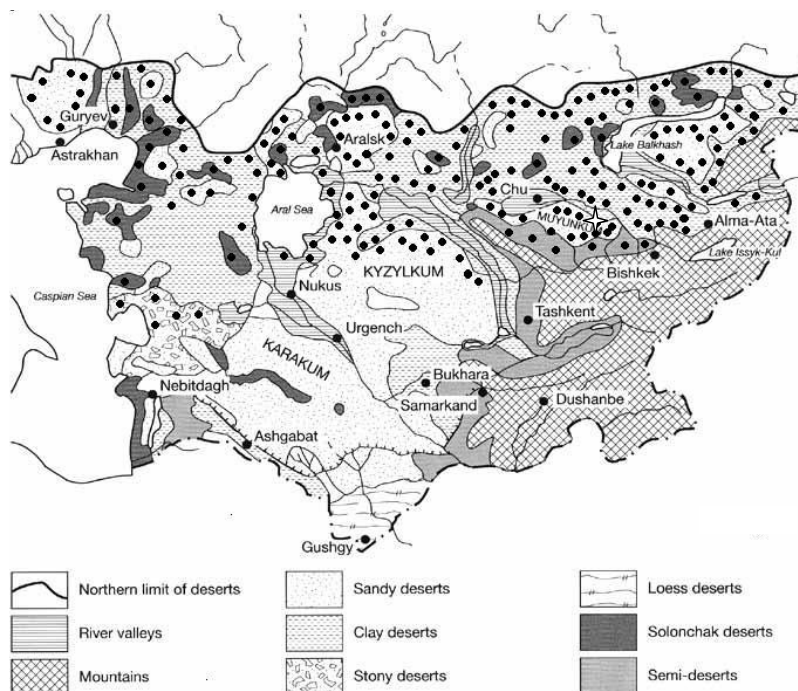
Figure 1a shows the broader desert ecoregions of Kazakhstan. Soil type and associated vegetation defines four desert types (MNRPE, 2009; World Wildlife Fund, 2011): sandy, clay, solonchak (salt) and stony deserts (Figure 2). These areas were identified from existing landscape maps (Lioubimsteva, 2002; UNDP, 2005), and samples collected from locations within each desert type. Plant nomenclature follows the conventions of International Plant Names Index (2012); Heteroptera nomenclature follows the catalogue of Aukema and Rieger (1995-2006).

### Desert types, soils and vegetation

The sandy desert of Kazakhstan occupies approximately 336 km<sup>2</sup>, or about 30% of the total desert area of the country (Figure 2). They are derived from ancient alluvial, coastal and deltaic deposits, located on the terrace-like, now arid plains. Dunes, ridges and sand hills are the most common topographic features, with mixed shrub-grass vegetation (Figure 3). Saxaul communities (*Haloxylon persicum* Bunge ex Boiss. & Buhse, *H. aphyllum* (Minkw.) Ilijin) are characteristic of sandy deserts, with endemic sand acacias (*Ammodendron*) also playing an important ecological role. These grow primarily on barchans (dunes or sand-hills), along with a diversity of shrub species such as *Calligonum leucocladum* (Schrenk) Bunge, *C. eriopodum* Bunge, and *C. setosum* Litv. (Chemonics International, 2001). Ephemeral cereals (*Poa*, *Bromus*), *Eremurus*, *Allium* and others form tussocks in the sandy soils, a characteristic of this desert type. Sandy deserts communities include many endemic plant species (*Salsola richteri* (Moq.) Kar. ex Litv., *S. subaphylla* C. A. Mey, *Ephedra strobilacea* Bunge, *Ferula foetida* (Bunge) Regel). In the northern desert ecoregion, where sandy soils are less common, Rachkovskaya (1995) describes the plant communities as primarily composed of semi-shrubs (*Ceratoides papposa* Botsch. & Ikonn. *Artemisia terrae-albae*, var. *massagetovii* Krasch., *A. santolina* Schrenk, and *A. songarica* Schrenk), shrubs (e.g. *Calligonum aphyllum* (Pall.) Guerke, *Ephedra lomatolepis* Schrenk), and sand-dependent grasses (*Agropyron fragil* (Roth) P. Candargy), white salsola (*Salsola arbuscula* (Pall.) Tzvelev) and sagebrush communities, with associated endemic species (*Artemisia kemrudica* Krasch., *A. diffusa* Krasch., *A. dimoana* Popov, *A. arenicola* Krasch. ex Poljak., *Mausolea eriocarpa* (Bunge) Podlech), are widespread on thin sandy soils and loamy sands. The endemic *Astragalus*



**Figure 1b.** Arid regions of Kazakhstan are a mosaic of clay, stone, salt and sandy deserts. The relief of the ecoregion is highly variable, ranging from alluvial plains to uplands cut with steep ravines, eroded plateaus and low mountains.



**Figure 2.** Location and extent of desert types of Kazakhstan and surrounding regions, with approximate locations of sampling stations (adapted from Lioubimsteva, 2002).



**Figure 3.** Sandy desert.



**Figure 4a.** Solonchak.

*vilosissimus* Bunge and shrub bindweed (*Convolvulus hammad* Steud.) are characteristic of the eastern part of region.

Solonchak is the salt desert of Kazakhstan, characterized by

solonetz soils, with a subsurface accumulation of sodium and magnesium salts and a significant amount of clay (Figure 4a,b). Salt deserts are formed where conditions that promote soil salinity,



**Figure 4b.** Solonchak detail.

alkalinity, or both are found (West, 1982). These are at the bottom of drainages in enclosed basins and where marine shales outcrop (West, 1982). In Central Asia, they are also found where saline ground waters are at or just below the surface creating highly saline solonetz soils (World Wildlife Fund, 2008). Salt-desert plant communities usually occur near playas or in other locations where they can access groundwater. In Kazakhstan solonchak deserts are found in alluvial saline plains, such as the low-lying maritime coastal plains of the Caspian and Aral seas, at the bottoms of depressions and around saline kettle lakes (such as Mynbulak in the Kyzylkum). Species of the salt-desert shrub complex have different degrees of tolerance to salinity and aridity, and tend to sort themselves out along a moisture/salinity gradient (West, 1982), creating a mosaic of plant communities. Specialized halophytic plant communities, including *Artemisia pauciflora* Weber ex Stechm., *A. schrenkiana* Ledeb., *A. nitrosa* Weber and perennial saltworts *Atriplex cana* C. A. Mey., *Anabasis salsa* (C. A. Meyer) Benth. ex Volken., and *Camphorosma monspeliaca* L. are characteristic of the highly saline plains of this desert group (World Wildlife Fund, 2008). Different types of sagebrush (*Artemisia terrae-albae semiarida* Krasch. et Lavr., *A. sublessingiana* Krasch. ex Poljakov) with characteristic salt grasses or solyanka (*Stipa sareptana* A.K. Becker, *S. kirghisorum* (Smirnov) Freitag, and the endemic *S. richterana* Karav. & Kir.) can be found throughout the region. Rachkovskaya (1995) and World Wildlife Fund (2011) report halophytic succulent semi-shrubs such as *Halimione verrucifera* (Bieb.) Aellen, *H. strobilaceum* (Pall.) Bieb., *Kalidium folitum* (Pall.) Moq., *K. schrenkianum* Bunge ex Ung.-Sternb., *Halostachys caspica* Meyer ex Schrenk, and *Halocnemum strobilaceum* (Pall.) Bieb., and annual saltworts, including species of *Petrosimonia*,

*Climacoptera*, *Suaeda microphylla* Pall., and *Salsola dendroides* Pall., which grow on solonchaks. Numerous rare plant species occur in the solonchak desert, such as *Artemisia lessingiana* Besser, *Stipa richterana* Karav. & Kir., *Ferula feruloides* Korov., and *Brachanthemum kasakhstanicum* Krasch. (World Wildlife Fund, 2008).

Clay deserts (takyr) (Figure 5a,b) are flat, unvegetated plains with a clay surface that is almost impermeable to water. Extensive ephemeral pools called sory form on the takyr during the spring rains. As they evaporate later in the season, they create the saline flats of hard, cracked clay. Clay deserts can be isolated or can occur in groups, and range from sparsely vegetated to completely barren. In Kazakhstan, the largest expanses of clay deserts are in the Ustyurt, plateau, in the littoral of the Aral Sea and Lake Balkhash, in the Betpak-Dala region between these, and in the Talasskiy Alatau and Karatau foothills (World Wildlife Fund, 2008). The perennial saltworts (*Salsola gemmascens* Pall., *S. orientalis* S. G. Gmel.) are the dominant plant species on clay soils. Other species associated with this desert type include *Anabasis salsa* (C.A.Mey.) Benth. ex Volken., salt grasses (*Stipa* sp.), yellow acacia (*Acacia farnesiana* (L.) Wild.), saxaul (*Haloxylon persicum* Bunge ex Boiss. & Buhse, *H. aphyllum* (Minkw.) Iljin), saltbush (*Salsola orientalis* S.G. Gmel., *S. laricifolia* Turcz. ex Litv.), and sagebrushes (*Artemisia terrae-albae* Krasch., *A. turanica* Krasch., and *A. gurganica* Krasch.).

Stony deserts (Figure 6a,b) have stone and gravel surfaces, while rock deserts are bare rock surfaces with large areas of pavement, kept clear of sand or gravel by wind. Vegetation is usually sparse, primarily lichens and desert moss attached to the hard surfaces. However, stony desert areas can support some vegetation: in areas where pockets of soil can accumulate, or



**Figure 5a.** Senior author collecting specimens on clay alluvial fan.



**Figure 5b.** Takyr (clay desert) detail.



**Figure 6a.** Stony desert.



**Figure 6b.** Stony desert detail.



where runoff from desert pavements concentrates in shallow runnels and washes cut into the pavement surface. In Kazakhstan, stony deserts are formed in low mountains, the melkosopochnik plateau and in the upper foothills of southern and western Kazakhstan, the result of rock weathering (World Wildlife Fund, 2008). Where they occur, the plant communities of the stony deserts are dominated by *Artemisia* sp., *Salsola arbuscula* Pall. and *Nanophyton erinaceum* (Pall.) Bunge.

### Sampling methods

Sampling locations were identified in each of the desert types and included sites in the Northern, Middle and South desert ecoregions (Figure 2). Specimens were collected by the senior author from sites within each of the desert regions between 1998 and 2009 using a mixture of standard Heteroptera collecting techniques (Coscarón et al., 2009; Fauvel, 1999). The per site active collecting effort was approximately 4 h, using a combination of sweeping, beating and collecting by hand. Additional "passive" samples were collected using Berlese funnels and barrier pitfall traps. Light traps were not used.

Where grasses or low vegetation were present, specimens were collected by sweeping an area systematically with a 38 cm diameter sweep net. The net bag was emptied every few minutes to prevent damage to collected specimens. Where larger vegetation was present, either in thickets or as individual bushes or trees, sweeping was supplemented by beating: rapping trunks and branches with a stick to dislodge and catch the insects in a 90 cm beating net when they fell. Hand collecting at all sites included searching on trunks, under bark, in leaf litter, under rocks and debris. Specimens were also extracted (using Berlese funnels) from soil samples taken at each sampling location from around the base of plants, beneath the leaf litter, from nearby loose soils, especially under rocks and debris. Both the number of samples and volumes collected at each site were variable. Barrier pitfall traps (up to 10 per site), consisting of four 11 cm traps connected in an X by a 2 crossed 1 m long x 10 cm high barriers (Hansen and New, 2005), were randomly placed in each sampling location. Traps were set in the afternoon and retrieved the following morning.

Identifications of collected specimen were verified using materials at the Institute of Zoology of the Kazakhstan Ministry of Education and Science and were deposited there.

### Statistical analysis

Because of the well-developed literature on similarity analysis using binary (presence-absence) data, methods from paleobiogeography and paleoecology were used for data analysis (Hammer et al., 2001) and interpretation.

Taxonomic organization of the Heteroptera follows Aukema and Rieger (1995-2006). Two similarity coefficients, the Jaccard index and the Sørensen-Dice index, were used to quantitatively assess affinities between Heteroptera species assemblages in pairs of desert types. The indices are calculated as follows:

$$J = C / [(S1+S2)-C] \text{ (Jaccard index)}$$

$$S-D = 2C / (S1+S2) \text{ (Sørensen-Dice index)}$$

Where, S1 and S2 are, respectively, the number of Heteroptera species present in each of the two compared desert types, C is the number of species shared between the desert types.

The Jaccard index is the most robust and informative of the suite

of many other similar metrics for measuring biogeographic similarities using binary (presence/absence) distribution data of taxa between areas (Shi, 1993). However, the Jaccard index is sensitive to sampling efficiency (sample size and quality of samples). Because the data were drawn, in part, from sources where sampling efficiency could not be determined, it was assumed unequal and a cross check was required. Biakov and Shi (2010) suggest a check for consistency and robustness of the Jaccard values can be made by comparing these to values calculated for the Sørensen-Dice similarity index. This index is one of the most reliable binary similarity measures next to the Jaccard index (Shi, 1993).

If the Jaccard's index is equal to one, all species are shared between the two communities. If the Jaccard's index is near 0, few if any species are shared. To determine the statistical significance of the level of Jaccard similarity between Heteroptera species assemblages in pairs of desert types, the calculated index values were compared to the critical index values provided by Real (1999). The probabilities associated with the index depend only on the number of species (N) reported from either of the two compared habitats (Real, 1999). To stay within the given range of the published table (Max. N value = 100), we used the lesser of the two species numbers in any of the pairwise desert type comparisons to establish N values.

For assemblages to be similar ( $H_0$  = no significant differences in assemblage species compositions in the pairwise comparisons, 1-tailed,  $p=.05$ ), the calculated Jaccard index values would have to be equal to or exceed the critical index value for a given value of N at  $p=.05$  (Real 1999). The null hypothesis ( $H_0$ ) is rejected when calculated Jaccard index values are less than the critical Jaccard index values.

## RESULTS

### Heteroptera species richness

We found 252 species of Heteroptera of 13 families in the Kazakh desert ecoregion (Table 1). The most species rich families were the Lygaeidae (55) and Miridae (48), which accounted for 41% of the reported species.

The species were distributed unevenly among the four desert types. The sandy desert was the most species rich, with 153 species in all 13 families. The solonchak desert was the next most species rich, with 101 species from all 13 families. The clay desert had 73 species and the stony desert, the most species poor, had 61 species. There were no species reported for the Piesmatidae or the Berytidae from clay and stony desert types.

### Similarity

Results for two similarity assessments are shown in Table 2. The values of the Sørensen-Dice similarity and Jaccard indices are highly correlated for Heteroptera assemblages for every pair of desert types compared ( $R^2 = 0.9999$  in both similarity assessments). The regression line is linear, indicating no significant deviations due to

**Table 1.** Family and species of Heteroptera reported from four desert types in Kazakhstan.

Taxa	Sandy desert	Clay desert	Solonchak	Stony desert
<b>Anthocoridae</b>				
<i>Orius agilis</i> Flor 1860			x	
<i>Orius albidipennis</i> Reuter 1884			x	
<i>Orius horvathi</i> Reuter 1884	x			
<i>Orius vicinus</i> Ribaut 1923	x	x	x	x
<i>Xylocoris halophilus</i> Kerzhner & Elov 1976			x	
<i>Xylocoris tesquorum</i> Kerzhner & Elov 1976			x	
Total: 6	2	1	5	1
<b>Nabidae</b>				
<i>Nabis palifer</i> Seidenstucker 1954	x	x		
<i>Nabis remanei</i> Kerzhner 1962			x	
<i>Nabis sareptanus</i> Dohrn 1862			x	
<i>Nabis sinoferus</i> sinoferus Hsiao 1964	x	x	x	x
Total: 4	2	2	3	1
<b>Miridae</b>				
<i>Atomophora pantherina</i> Reuter 1879	x	x		
<i>Atomoscelis onusta</i> Fieber 1861	x	x	x	
<i>Camptotylidea suturalis</i> Reuter 1903	x			
<i>Camptotylus bipunctatus</i> Reuter 1879	x			
<i>Chlamydatus eurotiae</i> Kerzhner 1962	x		x	
<i>Compsidolon pumilum</i> Jakovlev 1876	x			
<i>Conostethus hungaricus</i> Wagner 1941			x	
<i>Glaucopterum vilgus</i> V.G.Putshkov 1977	x			
<i>Hyoidea notaticeps</i> Reuter 1876	x			
<i>Leucopterum candidatum</i> Reuter 1879			x	
<i>Leucopterum pallens</i> Reuter 1879			x	
<i>Maurodactylus albidus</i> Kolenati 1845	x			
<i>Orthops pilosulus</i> Jakovlev 1877	x			x
<i>Orthotylus rubidus</i> Puton 1874			x	
<i>Orthotylus turanicus</i> Reuter 1883	x			
<i>Orthotylus virens</i> Fallen 1807			x	
<i>Phytocoris incanus</i> Fieber 1864		x		
<i>Phytocoris kazachstanicus</i> Muminov 1989	x			
<i>Phytocoris kyzylkumi</i> Muminov 1989	x			
<i>Phytocoris turkestanicus</i> Poppius 1912			x	
<i>Phytocoris undulatus</i> Reuter 1877	x			
<i>Polymerus brevicornis</i> Reuter 1879	x			
<i>Psallopsis kirgisica</i> Becker 1864			x	
<i>Psallopsis longicornis</i> Jakovlev 1902			x	
<i>Solenoxyphus fuscovenosus</i> Fieber 1864			x	
<i>Solenoxyphus lepidus</i> Puton 1874	x		x	
<i>Solenoxyphus punctipennis</i> Reuter 1879			x	
<i>Stenodema turanica</i> Reuter 1904	x	x		
<i>Trigonotylus brevipes</i> Jakovlev 1880			x	
<i>Trigonotylus ruficornis</i> Geoffroy 1785			x	

Table 1. Continued

<i>Tuponia arcufera</i> Reuter 1879		x			
<i>Tuponia concinna</i> Reuter 1875		x			
<i>Tuponia distincta</i> Drapolyuk 1980		x			
<i>Tuponia elegans</i> Jakovlev 1867				x	
<i>Tuponia jaxartensis</i> Drapolyuk 1980		x			
<i>Tuponia loginovae</i> Drapolyuk 1982		x			
<i>Tuponia mixticolor</i> A.Costa 1862		x			
<i>Tuponia persica</i> Wagner 1957		x			
<i>Tuponia prasina</i> Fieber 1864		x			
<i>Tuponia roseipennis</i> Reuter 1878		x			
<i>Tuponia soongorica</i> Drapolyuk 1980		x			
<i>Tuponia spinifera</i> Drapolyuk 1982		x			
<i>Tuponia suturalis statices</i> Jakovlev 1906		x			
<i>Tuponia suturalis suturalis</i> Reuter 1901		x		x	
<i>Tuponia tibialis</i> Reuter 1901		x			
<i>Voruchiella haloxylis</i> V.G.Putshkov 1984		x			
<i>Voruchiella pallida</i> Reuter 1878		x			
<i>Voruchiella plagiata</i> Poppius 1912		x			
Total: 48	17	21	17	1	
<b>Reduviidae</b>					
<i>Coranus subapterus</i> De Geer 1773					x
<i>Empicoris culiciformis</i> De Geer 1773	x				
<i>Holotrichius bergrothi</i> Reuter 1891	x	x	x		x
<i>Holotrichius ilius</i> Dispons 1964	x				
<i>Holotrichius kizilkumi</i> Dispons 1964	x				
<i>Holotrichius mesoleucus</i> Kiritshenko 1914	x				
<i>Holotrichius tristis</i> Jakovlev 1874	x		x		
<i>Oncocephalus impictipes</i> Jakovlev 1885	x				
<i>Pasira basiptera</i> Stal 1859	x		x		x
<i>Ploiaria turkestanica</i> P.V.Putshkov 1984	x				
<i>Reduvius disciger</i> Horvath 1896	x				x
<i>Reduvius elegans</i> Jakovlev 1885	x				
<i>Reduvius tenuicornis</i> Jakovlev 1889	x				
<i>Reduvius testaceus</i> Herrich-Schaeffer 1845	x	x	x		x
<i>Vachiria prolixa</i> Kiritshenko 1925	x	x	x		x
Total: 15	14	3	5	6	
<b>Tingidae</b>					
<i>Agramma atricapillum</i> Spinola 1837			x		
<i>Agramma brevirostre</i> Jakovlev 1901			x		
<i>Catoplatus cathusianus</i> Goeze 1778	x				
<i>Dictyonota atraphaxius</i> Golub 1975	x				
<i>Dictyonota ephedrae</i> Kerzhner 1964	x	x			
<i>Dictyonota halimodendri</i> Golub 1975			x		x
<i>Dictyonota horvathi</i> Kiritshenko 1914	x	x	x		
<i>Dictyonota kerzhneri</i> Golub 1975		x			
<i>Dictyonota rectipilis</i> Asanova 1970	x		x		
<i>Dictyonota salsolae</i> Golub 1975		x			
<i>Dictyonota sareptana</i> Jakovlev 1874	x	x	x		x
<i>Kalama henschi</i> Puton 1892					x

Table 1. Continued

<i>Kalama tricornis</i> Schrank 1801	x	x	x	x
<i>Oncochila scapularis</i> Fieber 1844	x			
<i>Tingis biseriata</i> Horvath 1902	x	x	x	x
<i>Tingis grisea</i> Germar 1835	x	x		x
<i>Tingis pauperata</i> Puton 1879	x	x		
<i>Tingis pusilla</i> Jakovlev 1873	x			
Total: 18	12	9	8	6
<b>Coreidae</b>				
<i>Bothrostethus annulipes</i> Herrich-Schaeffer 1835	x		x	x
<i>Centrocoris spiniger</i> Fabricius 1781	x	x	x	x
<i>Cercinthinus annulipes</i> Kiritshenko 1916	x			
<i>Coriomeris scabrocornis scabrocornis</i> Panzer 1805		x		
<i>Coriomeris vitticollis</i> Reuter 1900		x		
<i>Enoplops disciger</i> Kolenati 1845	x			
<i>Haploprocta bicolor</i> Kiritshenko 1911	x			
<i>Haploprocta pustulifera</i> Stal 1860	x			
<i>Phyllomorpha lacerata</i> Herrich-Schaeffer 1835	x	x		x
Total: 9	7	4	2	3
<b>Rhopalidae</b>				
<i>Agrophopus lethierryi</i> Stal 1872	x	x	x	
<i>Agrophopus suturalis</i> Reuter 1900	x			
<i>Brachycarenum tigrinus</i> Schilling 1829	x	x		x
<i>Chorosoma gracile</i> Josifov 1968	x			
<i>Chorosoma longicolle</i> Reuter 1900	x			
<i>Chorosoma schillingii</i> Schilling 1829	x			
<i>Leptoceraea femoralis</i> Horvath 1897	x		x	
<i>Leptoceraea viridis</i> Jakovlev 1873			x	
<i>Maccevethus corsicus persicus</i> Jakovlev 1882	x		x	
<i>Myrmus glabellus</i> Horvath 1901	x			
<i>Stictopleurus abutilon</i> Rossi 1790	x			x
<i>Stictopleurus angustus</i> Reuter 1900	x			x
<i>Stictopleurus murinus</i> V.G.Putshkov 1978				x
Total: 13	11	2	4	4
<b>Berytidae</b>				
<i>Berytinus geniculatus</i> Horvath 1885			x	
<i>Berytinus signoreti</i> Fieber 1859	x			
<i>Gampsocoris punctipes punctipes</i> Germar 1822	x			
Total: 3	2	0	1	0
<b>Lygaeidae</b>				
<i>Artheneis alutacea</i> Fieber 1861			x	
<i>Bianchiella sarmatica</i> Kiritshenko 1926	x			
<i>Bleteogonus beckeri</i> Frey-Gessner 1863	x			
<i>Bleteogonus circumcinctus</i> Reuter 1885	x			
<i>Blissus putoni</i> Jakovlev 1875	x			
<i>Bogdiana myrmica</i> Kerzhner 1964			x	
<i>Camptocera glaberrima</i> Walker 1872	x	x	x	x
<i>Diomphalus hispidulus</i> Fieber 1864	x		x	x
<i>Cymophyes golodnajana</i> Seidenstucker 1953			x	
<i>Cymophyes ochroleuca</i> Fieber 1870			x	

Table 1. Continued.

<i>Emblethis angustus</i> Montandon 1890				x
<i>Emblethis brachynotus</i> Horvath 1897				x
<i>Emblethis denticollis</i> Horvath 1878	x	x	x	x
<i>Emblethis dilaticollis</i> Jakovlev 1874				x
<i>Emblethis verbasci</i> Fabricius 1803	x	x	x	x
<i>Engistus salinus</i> Jakovlev 1874			x	
<i>Geocoris arenarius</i> Jakovlev 1867			x	
<i>Geocoris aspasia</i> Linnavuori 1972	x			
<i>Geocoris chloroticus</i> Puton 1888				x
<i>Geocoris desertorum</i> Jakovlev 1871	x	x	x	x
<i>Geocoris dispar</i> Waga 1839				x
<i>Geocoris erythrocephalus</i> Lepeletier & Serville 1825	x	x	x	x
<i>Geocoris grylloides</i> Linnaeus 17610				x
<i>Geocoris hirticornis</i> Jakovlev 1882	x			
<i>Geocoris limbatellus</i> Horvath 1895				x
<i>Geocoris megacephalus</i> Rossi 1790	x	x	x	x
<i>Geocoris pattakumenis</i> Kiritshenko 1914	x			
<i>Geocoris pubescens</i> Jakovlev 1871	x	x	x	x
<i>Graptopeltus validus</i> Horvath 1875		x		x
<i>Henestaris halophilus</i> Burmeister 1835			x	
<i>Horvathiolus heydeni</i> Puton 1892	x	x	x	x
<i>Horvathiolus syriacus</i> Reuter 1885	x			
<i>Hyalocoris pilicornis</i> Jakovlev 1874	x			
<i>Icus angularis</i> Fieber 1861				x
<i>Ischnopeza hirticornis</i> Herrich-Schaffer 1850				x
<i>Jakowleffia setulosa</i> Jakovlev 1874	x			
<i>Lamprodema maura</i> Fabricius 1803			x	
<i>Leptodemus minutus</i> Jakovlev 1874				x
<i>Lethaeus picipes</i> Herrich-Schaeffer 1850				x
<i>Lygaeosoma anatolicum</i> Seidenstucker 1960			x	
<i>Lygaeus murinus</i> Kiritshenko 1914	x			
<i>Megalonotus puncticollis</i> Lucas 1849				x
<i>Melanocoryphus albomaculatus</i> Goeze 1778	x			
<i>Microplax interrupta</i> Fieber 1837				x
<i>Nysius cymoides</i> Spinola 1837			x	
<i>Nysius thymi thymi</i> Wolff 1804	x		x	
<i>Oxycarenus pallens</i> Herrich-Schaeffer 1850	x			x
<i>Paranysius fraterculus fraterculus</i> Horvath 1895	x			
<i>Pionosomus horvathi</i> Vinokurov 1982				x
<i>Pionosomus opacellus</i> Horvath 1895			x	
<i>Plinthisus longicollis</i> Fieber 1861				x
<i>Plinthisus ptilioides</i> Puton 1874	x	x	x	x
<i>Trapezonotus inglorius</i> Vinokurov 1990			x	
<i>Tropidophlebia costalis</i> Herrich-Schaffer 1850	x			
<i>Xanthochilus turanicus</i> Wagner 1961	x	x	x	x
Total: 55	27	11	24	28
<b>Cydnidae</b>				
<i>Aethus hispidulus</i> Klug 1845	x	x	x	x
<i>Aethus pilosus</i> Herrich-Schaeffer 1834	x			

Table 1. Continued.

<i>Byrsinus laeviceps</i> Kerzhner 1972	x			
<i>Byrsinus pilosulus</i> Klug 1845	x		x	
<i>Byrsinus rugosus</i> Jakovlev 1874	x		x	
<i>Byrsinus comaroffii</i> Jakovlev 1879	x		x	x
<i>Byrsinus discus</i> Jakovlev 1906	x			
<i>Byrsinus flavicornis</i> Fabricius 1794	x			
<i>Byrsinus fossor</i> Mulsant & Rey 1866	x			
<i>Byrsinus penicillatus</i> Wagner 1964	x			
<i>Canthophorus mixtus</i> Asanova 1964		x		x
<i>Canthophorus coeruleus</i> Reuter 1902		x		
<i>Exosehirus validus</i> Jakovlev 1877	x	x	x	
<i>Geotomus ciliatitylus</i> Signoretta 1883	x			
<i>Geotomus elongatus</i> Herrich-Schaeffer 1840	x		x	
<i>Linospa candida</i> Horvath 1889	x	x		
<i>Linospa orbicularis</i> Jakovlev 1885	x	x		
<i>Microporus nigrita</i> Fabricius 1794	x			
<i>Ochetostethus nanus</i> Herrich-Schaeffer 1834	x			
<i>Stibaropus henkei</i> Jakovlev 1874	x			
<i>Stibaropus hohlbecki</i> Kiritshenko 1912	x			
Total: 21	19	6	6	3
<b>Pentatomidae</b>				
<i>Aelia acuminata</i> Linnaeus 1758	x			
<i>Aelia furcula</i> Fieber 1868		x		
<i>Anthemina lunulata</i> Goeze 1778	x			
<i>Anthemina pusio pusio</i> Kolenati 1846	x			x
<i>Brachynema germari</i> Kolenati 1846	x	x	x	x
<i>Brachynema signatum</i> Jakovlev 1779			x	
<i>Capnoda batesoni</i> Jakovlev 1889	x	x		
<i>Carpocoris coreanus</i> Distant 1899	x			
<i>Cellobius abdominalis</i> Jakovlev 1885			x	
<i>Chroantha ornatula</i> Herrich-Schaeffer 1842			x	
<i>Crypsinus angustatus</i> Baerensprung 1859	x			
<i>Desertomenida albula</i> Kiritshenko 1914	x		x	
<i>Desertomenida jakowleffi</i> Horvath 1907	x		x	
<i>Desertomenida quadrimaculata</i> Horvath 1892	x		x	
<i>Eurydema fieberi</i> Fieber 1837				x
<i>Eurydema maracandica</i> Oshanin 1871	x			
<i>Eurydema wilkinsi</i> Distant 1879	x			
<i>Leprosoma tuberculatum</i> Jakovlev 1874	x	x		
<i>Menaccarus arenicola</i> Scholtz 1847	x			
<i>Menaccarus deserticola</i> Jakovlev 1900	x			
<i>Menaccarus dohrnianus</i> Mulsant & Rey 1866	x			
<i>Ochyrotylus helvinus</i> Jakovlev 1885	x	x	x	
<i>Sciocoris capitatus</i> Jakovlev 1882			x	
<i>Putonia asiatica</i> Jakovlev 1885			x	
<i>Sciocoris cursitans cursitans</i> Fabricius 1794	x			
<i>Sciocoris deltacephalus</i> Fieber 1861	x	x	x	
<i>Sciocoris homalonotus</i> Fieber 1851				x
<i>Sciocoris macrocephalus</i> Fieber 1851	x			

Table 1. Continued.

<i>Sciocoris maculatus</i> Fieber 1851	x			
<i>Sciocoris sulcatus</i> Fieber 1851	x	x		x
<i>Tarisa elevata</i> Reuter 1901			x	x
<i>Tarisa pallescens</i> Jakovlev 1871			x	
<i>Tarisa salsae</i> Kerzhner 1964			x	
<i>Tarisa subspinosa subspinosa</i> Germar 1839			x	
<i>Tarisa virescens</i> Herrich-Schaeffer 1851			x	
<i>Thologmus flavolineatus</i> Fabricius 1798	x	x		
<i>Ventocoris balassogloi</i> Horvath 1889			x	
<i>Ventocoris productus</i> Jakovlev 1885			x	
Total: 38	23	8	18	6
<b>Scutelleridae</b>				
<i>Ellipsocoris tamerlani</i> Kiritshenko 1914	x			
<i>Irochrotus lanatus</i> Pallas 1773	x			
<i>Irochrotus turanicus</i> Kerzhner 1976	x	x	x	x
<i>Melanodema carbonaria</i> Jakovlev 1880	x			
<i>Odontoscelis byrrhus</i> Seidenstucker 1972	x	x	x	
<i>Odontoscelis dorsalis</i> Fabricius 1798	x	x		
<i>Odontoscelis fuliginosa</i> Linnaeus 1761	x	x	x	
<i>Odontoscelis zarudnyi</i> V.G.Putshkov 1965	x	x		x
<i>Odontotarsus angustatus</i> Jakovlev 1880	x			
<i>Odontotarsus impictus</i> Jakovlev 1886	x			
<i>Odontotarsus obsoletus obsoletus</i> Horvath 1906	x			
<i>Odontotarsus rufescens</i> Fieber 1861	x			
<i>Periphima batesoni</i> Jakovlev 1889	x			
<i>Phimodera bergi</i> Jakovlev 1905	x			
<i>Phimodera fumosa</i> Fieber 1863	x			
<i>Polyphima koenigi</i> Jakovlev 1889	x	x		
Total: 16	16	6	3	2
<b>Piesmatidae</b>				
<i>Parapiesma kochiae</i> Becker 1867			x	
<i>Parapiesma kolenatii</i> Fieber 1861			x	
<i>Parapiesma salsolae</i> Becker 1867			x	
<i>Parapiesma variabile</i> Fieber 1844	x			
<i>Piesma capitatum</i> Wolff 1804			x	
<i>Piesma maculatum</i> Laporte 1833			x	
Total: 6	1	0	5	0
TOTAL Species 252	153	73	101	61

underlying differences in sampling efficiency.

Table 2 shows the results for test for overall Jaccard similarity among assemblages, where C is the number of shared species. The first test included the ubiquitous generalist species in the pairwise comparisons. In the second test, the shared species value C includes only species that shared just the two habitat pairs evaluated, excluding all generalist species. The null hypothesis for

both tests is:  $H_0$  = no significant differences in assemblage species compositions in the pairwise comparisons, 1-tailed,  $p=0.05$ .

The two tests for Jaccard similarity showed different results. In the first test, for overall similarity (including generalist species), the calculated Jaccard index values (Table 2) were less than the critical index values of Real (1999) for all six pair wise comparisons of Heteroptera

**Table 2.** Jaccard index and Sørensen-Dice index values for Heteroptera similarity between pairs of Kazakh desert types.

Desert type pairs	SpA	SpB	C	Sørensen-Dice	Jaccard	N	J <sub>p=.05</sub>
<b>Including habitat generalist species</b>							
Sandy-Clay	153	73	46	0.4089	0.2570	73	0.4384
Sandy-Solonchak	153	101	45	0.3529	0.2143	101	0.4081
Sandy-Stony	153	61	37	0.3474	0.2102	61	0.4426
Clay -Solonchak	73	101	32	0.3860	0.2222	73	0.4384
Clay-Stony	73	61	29	0.4366	0.2762	61	0.4426
Solonchak-Stony	101	61	28	0.3313	0.2059	61	0.4426
<b>Without habitat generalist species</b>							
Sandy-Clay	153	73	12	0.1062	0.0561*	73	0.4384
Sandy-Solonchak	153	101	13	0.1024	0.0539*	101	0.4081
Sandy-Stony	153	61	6	0.0561	0.0288	61	0.4426
Clay-Solonchak	73	101	1	0.0115	0.0058	73	0.4384
Clay-Stony	73	61	2	0.0299	0.0152	61	0.4426
Solonchak-Stony	101	61	2	0.0247	0.0125	61	0.4426

SpA = number of species in the first desert type; SpB = number of species in the second desert type; C = number of shared species; N = number of species in the desert type with the lesser number of species; J<sub>p=.05</sub> is the critical value of the Jaccard index for that N value (Real, 1999).

assemblages. By rejecting the null hypothesis ( $H_0$ ), we concluded that there were significant differences in Heteroptera species assemblages among all four desert types.

However, tests for similarity that excluded ubiquitous generalist species (Table 2) showed similar Heteroptera assemblages in two pairs of desert types. Sandy desert Heteroptera assemblages were statistically similar ( $p > .05$ ) to both the clay desert and to solonchak desert assemblages.

### Habitat specialists and habitat generalists

A large number of species were found in just one desert type and not others, while other species were ubiquitous and found in all four desert types (Table 1). To determine how differences in distribution of species among desert types may influence similarity, we assigned all desert Heteroptera species into one of three groups. Habitat generalist species were collected from three or four of the desert types; habitat specialist species were collected from only one of the four desert types. The remaining species, collected from two desert types, were indeterminate in habitat specialization and classified as intermediate species.

There were significant differences in the proportions of habitat generalist and habitat specialist species among the four desert types ( $X^2=22.1$ ,  $df = 3$ ,  $.001 < p$ ). Habitat

specialist species, limited to only one of the four desert types, dominate the Heteropteran fauna of Kazakh deserts (Figure 7). There were 175 habitat specialist species, about 69% of the total number of reported species, with at least one habitat specialist species in each family. There were many fewer habitat generalist species (38), and in fewer families (11). The Berytidae and Piesmatidae had no habitat generalist species. The remaining 38 species co-occurred in two of the desert types.

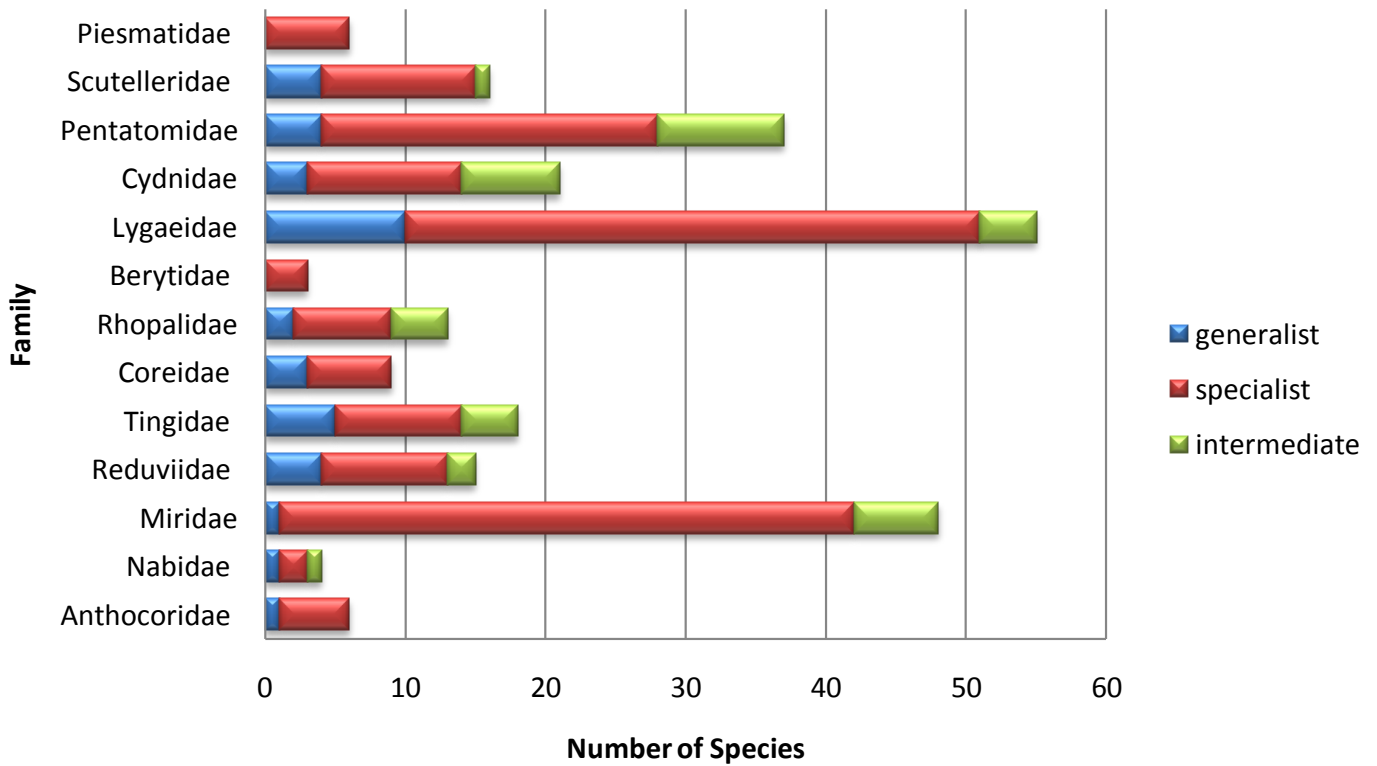
We also found significant differences in the proportions of habitat generalist and habitat specialist species among Heteroptera families ( $X^2=14.3$ ,  $df = 7$ ,  $.05 \leq p \leq .10$ ). The number of habitat generalist, intermediate and habitat specialist species by family is shown in Table 3. Two smaller families, with only a few species, Berytidae (3 species) and Piesmatidae (6 species) had only habitat specialist species. Of the second most species rich family, the Miridae, 85% (41/48) were habitat specialists. The Lygaeidae, the most species rich family, had a slightly lower proportion of habitat specialist species (41/55, or 75%).

Habitat specialist species were unevenly distributed among the four desert types (Figure 8). The proportion of habitat specialist species was greater in the more species rich desert types than in the species poor deserts. Sandy deserts had the highest proportion of habitat specialist species (83/153 or 54%), followed closely by solonchak (51/101 or 50%), while the clay and stony deserts had the



**Table 3.** Habitat specialist, habitat generalist and intermediate Heteroptera species, by family (Habitat specialists are species limited to one desert habitat type, intermediate species limited to two, generalists found in 3 to 4 habitat types).

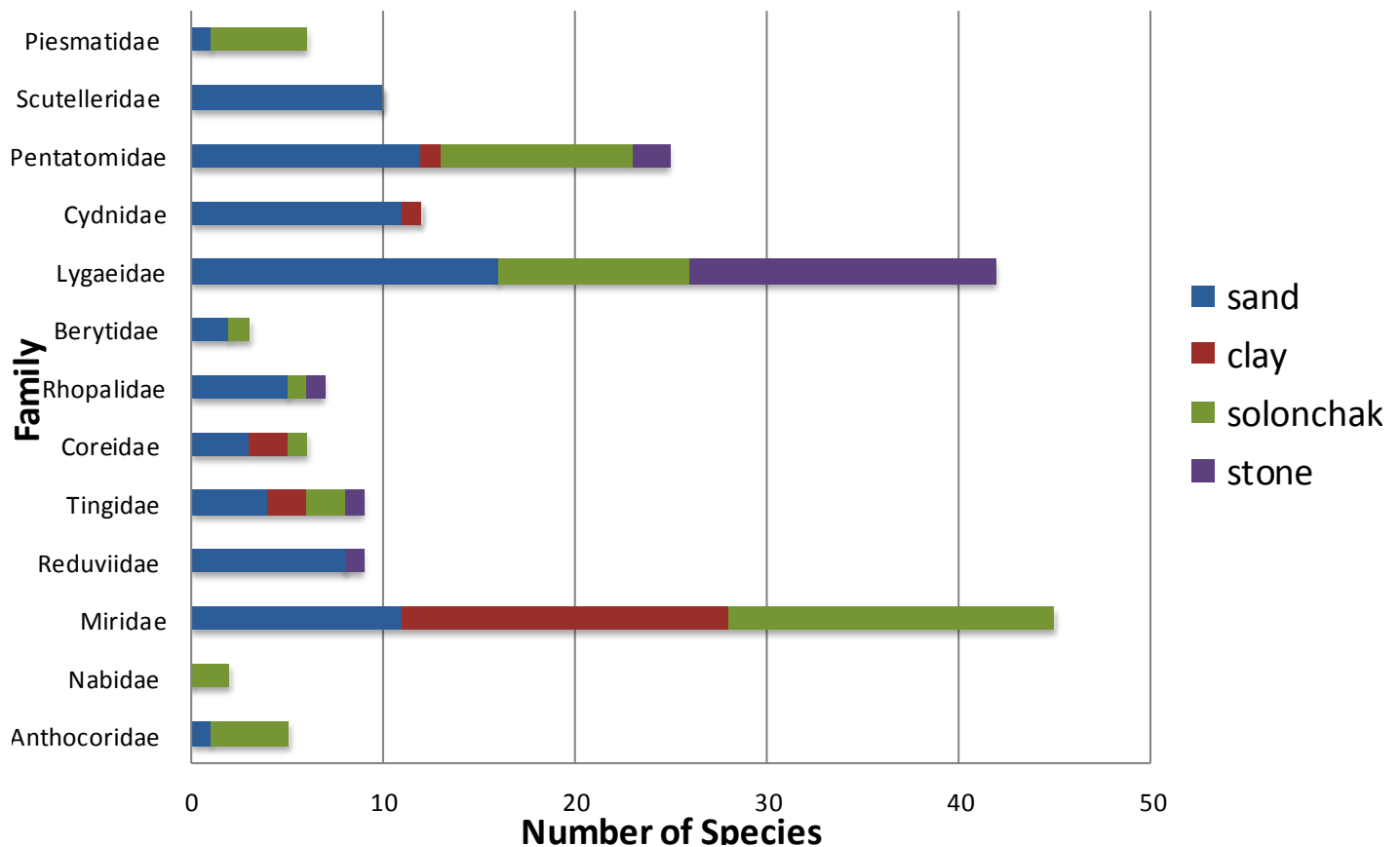
Family	Generalist	Specialist	Intermediate	Total
Anthocoridae	1	5	0	6
Nabidae	1	2	1	4
Miridae	1	41	6	48
Reduviidae	4	9	2	15
Tingidae	5	9	4	18
Coreidae	3	6	0	9
Rhopalidae	2	7	4	13
Berytidae	0	3	0	3
Lygaeidae	10	41	4	55
Cydnidae	3	11	7	21
Pentatomidae	4	24	9	38
Scutelleridae	4	11	1	16
Piesmatidae	0	6	0	6
<b>Total</b>				252



**Figure 7.** Numbers of habitat generalist, habitat specialist and intermediate Heteroptera species by family.

lowest (32 and 31% respectively). Two families with relatively few habitat specialist species (Piesmatidae,

Anthocoridae) had the most representatives in the solonchak desert. Nearly all of the habitat specialist



**Figure 8.** Number of habitat specialist Heteroptera species, by family, among desert types.

species of the families Scutelleridae, Pentatomidae, Cydnidae, Tingidae, and Reduviidae are associated with the sandy desert type.

Two families, Lygaeidae and Miridae, had the highest number of habitat specialist species, 41 each restricted to only one desert type. However, neither family was strongly associated with any one desert type (Figure 8). The 41 Lygaeid habitat specialists were fairly evenly distributed among three of the four desert types, with 14, (34%) 12 (29%), and 15 (37%) found in the sandy, solonchak and stony deserts. The Lygaeidae were the only family to have a large proportion of habitat specialist species in the stony desert (15 of the 20 reported specialist species). At the same time, there were no Lygaeid habitat specialists in the clay desert.

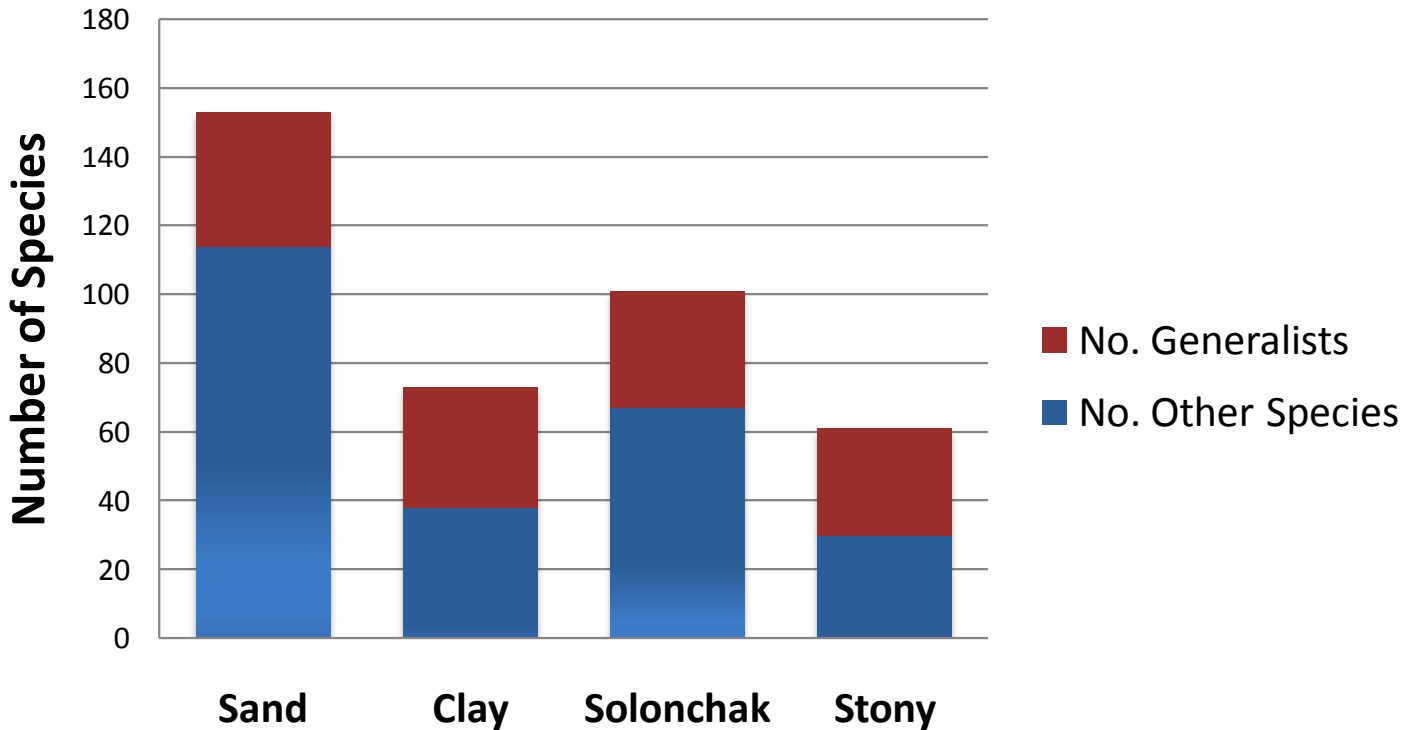
Members of the Miridae were highly habitat specialized, with only one habitat generalist species, but 41 species were limited to only one desert type: 11 in the sandy desert, 16 in the solonchak desert and 17 in the clay desert. The Miridae form the largest proportion of habitat specialist species in this desert type (17/23, or 74%),

where specialist species of nearly all the other families are absent. In contrast, no habitat specialist Miridae species were reported from stony deserts, where the Lygaeidae are numerous but habitat specialists of other families are poorly represented.

Habitat generalist species formed a greater proportion of the Heteropteran fauna in the two most species-poor deserts (Figure 9). Habitat generalist species were 51% (31/61) of the stony desert fauna, and 52% (35/73) of the clay desert, but were only 34 and 25% of the fauna in the more species rich solonchak and sandy deserts respectively. There was no significant correlation between total species number and number of generalist species by desert type (Pearson's Correlation Coefficient,  $r = .5954$ ,  $t = 1.048$ ,  $p > .10$ ).

## DISCUSSION

The Heteroptera are one of the more distinctive orders of insects, inhabiting a diversity of habitats and playing an



**Figure 9.** A comparison of the proportions of habitat generalist species against total species by desert type.

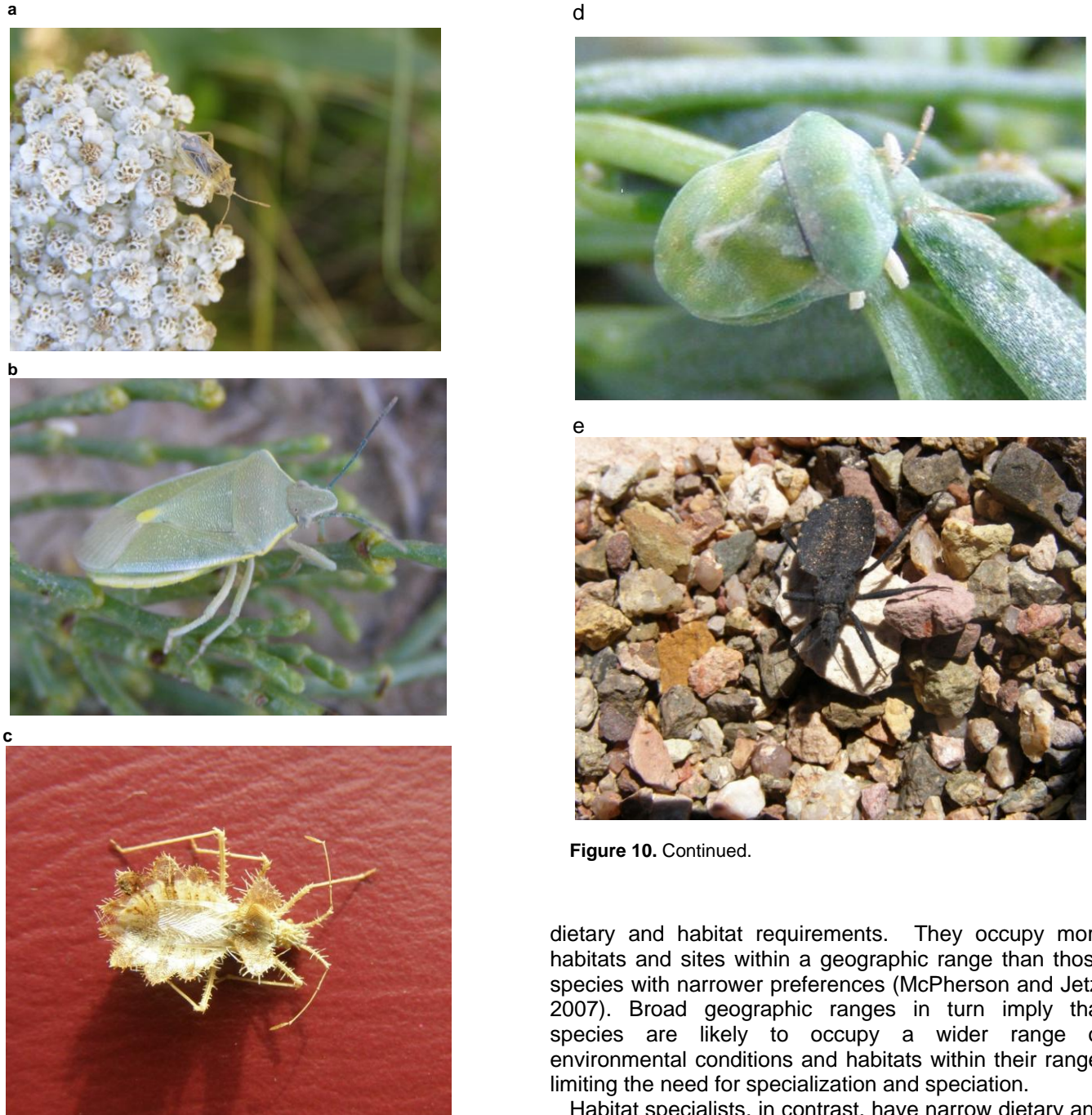
important role in ecosystem processes. True bugs have important functional roles as predators and herbivores, and are important indicators of overall arthropod species richness within one habitat (Duelli and Obrist, 1998; Ullrich 2001). The distribution of Heteroptera is strongly influenced by climate and vegetation (Dolling, 1991), as well as geology and soil types and vegetation characteristics, making them a valuable indicator species habitats than those species with broad preferences and occupy a narrower range of environmental conditions and habitats within their range (McPherson and Jetz 2007). Endemics are often associated with narrow and limited for overall insect biodiversity. Their sensitivity to environmental factors make Heteroptera good indicators of ecological variation (Fauvel, 1999), with changes in species composition or populations indicators of various disturbances. Because of their high degree of host-plant specialization and their feeding habits, differences in the distribution of true bugs among similar habitats may indicate subtle effects of environmental differences (Sobek et al., 2009).

Yesenbekova (2011) gave the total number of desert Heteroptera from Kazakhstan as 405 species, with 158 species from Kazakhstan’s sandy deserts, 105 species in the solonchak deserts, 75 species in the clay deserts, and 67 species in the stony deserts. These agree closely

with our results: the sandy desert with 152 species, solonchak desert with 103 species, clay desert with 73 species and the stony desert with 61 species. However, Yesenbekova's (2011) total is inaccurate in that it simply aggregates the species counts from each of the four desert types, thus counting species reported from more than one desert type more than once. The species list reported here is corrected to count each species only once, and to correct other double counts.

We found the desert Heteroptera assemblages of Kazakhstan to be both species rich and with large proportions of specialized species limited to just one desert type, with relatively few generalist species. Some characteristic Heteroptera of the Kazakh deserts are shown in Figure 10. The type of desert examined had a significant effect on the number of species present and on the proportion of specialist and generalist species. The sandy desert was the most species rich (153 species), followed by the solonchak desert (101 species). The clay desert had markedly fewer species (73) than either the sandy or solonchak deserts. The stony desert was the most species poor, with only 61 species.

Occurrence patterns can be used to quantify species as ecological habitat generalists or habitat specialists (Devictor et al., 2010). Habitat generalist species have relatively broad environmental tolerances, with broad



**Figure 10.** Some characteristic Heteroptera of Kazakh deserts. **a.** *Brachycarenum tigrinus*, a polyphagous habitat generalist common in takyr (clay desert). **b.** *Brachynema germari* is a polyphagous habitat generalist found in all desert types. **c.** *Phyllomorpha lacerata* is a soil burrowing, sand associated species found in sandy and solonchak deserts. **e.** *Holotrichiis bergrothi* is a habitat generalist predator, one of the more common species of the stony desert. **d.** *Tarisa elevata* is associated with alkaline-saline vegetation of the solonchak desert.

**Figure 10.** Continued.

dietary and habitat requirements. They occupy more habitats and sites within a geographic range than those species with narrower preferences (McPherson and Jetz, 2007). Broad geographic ranges in turn imply that species are likely to occupy a wider range of environmental conditions and habitats within their range, limiting the need for specialization and speciation.

Habitat specialists, in contrast, have narrow dietary and habitat requirements. Because they have relatively limited environmental tolerances they occupy fewer conditions within a taxon's geographic range.

Arthropod diversity in sandy deserts has been reported to be high (Whitford, 2002). Konstantinov et al. (2009) reported the highest diversity of three families of Coleoptera from sandy desert sites in the Transolonchakai Gobi. In the Arabian Desert, Tigar and Osborne (1997) found higher ground arthropod diversity in sand sites than gravel sites. In the northern Chihuahua

Desert, Crawford (1988) found species richness and abundance of various insect taxa to be higher in sand dune habitats than in areas with sandy loam soils, or vegetation cover of two shrub species or mixed grasses. Ayal et al. (2005) suggest that habitat-substrate specialization drives the higher than expected diversity of desert insects in the sand regions of the Negev Desert.

Desert types are classified by vegetation, which reflects moisture conditions, and by soils, which determine available soil moisture (Whitford, 2002). Desert areas with more available water (as precipitation, groundwater) have more abundant and diverse vegetation, which in turn supports a larger number of desert arthropod taxa (Schowalter et al., 1999). Where vegetation is sparse, desert arthropod species richness declines (Ayal et al., 2005; Floyd, 1996;).

Vegetation increases Heteroptera diversity (Sobek et al., 2009; Ullrich, 2001); with vegetation structure and flower abundance identified as key factors in Heteroptera species richness, abundance and community composition (Zurbrugg and Frank, 2006). Experimental studies of desert grassland insect assemblages found that increased plant diversity increased arthropod species richness (Forbes et al., 2005). Whitford (2002) reviewed research linking desert arthropod diversity and abundance to structure biomass, moisture content and nutritional value of the shrub canopy, ephemerals and grasses. Experimental manipulation of desert shrub cover showed that vegetation increases diversity of desert arthropods by reducing predation (Floyd 1996; Ayal et al., 2005).

Crawford (1988) proposed that the soil texture and microenvironment of desert sands are more suitable habitats than compacted substrates for desert ground dwelling arthropods, especially when conditions are extreme. Sand is a poor heat conductor, so even shallow depths provide refuges from thermal extremes at the surface. Sand has a high infiltration rate, so its porosity allows water to accumulate at depths below the surface zone of intense evaporation. Finally, sand is easily burrowed, allowing adapted species to access these refuges.

The sandy deserts of Kazakhstan, where we found the highest Heteroptera species richness and proportion of habitat specialists, have the highest plant diversity, biomass and vegetative cover of all of the desert types (Lioubimsteva, 2002). While more limited than sandy desert plant communities, solonchak vegetation can be locally extensive and productive, and supported the second highest number of species and proportion of habitat specialists found in this study. In clay and stony deserts, with the highest proportion of generalist species and the lowest numbers of taxa, Lioubimsteva (2002) reports much sparser and much less diverse plant

communities. Sandy deserts also share a number of Heteroptera species with both solonchak (13) and clay (12) deserts.

Sand deserts have a greater abundance and diversity of vegetation compared to the other desert types, with soils, topography, and soil moisture content the key factors affecting the composition and distribution of vegetation.

Permeability and texture of sandy soils permit precipitation to be absorbed and to infiltrate deeply. In deep sands, this allows water to accumulate below the zone of intense evaporation, supporting deep rooted perennials. (McAuliffe, 2000; Whitford, 2002). The higher diversity and abundance of perennials in sandy deserts provides a greater and more predictable plant resource base capable of supporting higher diversity of herbivorous insects (Whitford, 2002). The increased structural diversity provided by the scrub vegetation of sandy deserts may also play a role. Central Asian sandy desert scrub vegetation is often in two tiers (Makhmudov, 2001). White saxaul (*Haloxylon persicum* Bunge ex Boiss. & Buhse), sand acacia (*Caragana*), sand thistle (*Salsola*), *Ephedra*, brush buckwheat (*Calligonum*), *Astragalus*, *Atraphaxis*, and various sage species (*Artemisia*) form the upper layer. Ephemerals, including species of *Iris*, *Aristida* and *Ferula* may also grow into the upper tier. The lower tier is composed of ephemerals, including *Eremerus*, *Ferula*, *Corispermum leptopterum* Iljin, sedges (*Carex*), grasses (*Poa bulbosa* L., *Agropyron fragile* (Roth) Nevski, *Stipa capillata* L.), dwarf rhubarb (*Rheum nanum* Siev. ex Pall.), various species of *Allium* and *Tulipa*, and genera of crucifers, legumes (Fabaceae) and others. However, species composition of any given patch of vegetation in the landscape is unpredictable (Whitford, 2002), and Heteropteran fauna in any given patch may range from species rich to species poor.

Sand is a poor conductor of heat and provides shelter from temperature extremes (Crawford, 1988). In sandy deserts, most herbivorous Heteroptera escape harsh daytime surface conditions by burrowing, primarily in leaf litter and in the loose soil around the bases of shrubs and grasses, emerging at night (Whitford, 2002). Diurnal species found on perennial vegetation move up and down in the canopy throughout the day to take advantage of moderate microclimates.

Species of the family Cydnidae are especially adapted for life in loose sandy soil. In this study, Cydnidae were the most species rich in the sandy desert, with many sand specialized species, including *Stibaropus hohlbecki*, *S. henkei*, *Aethus hispidulus*, *A. pilosus*, *Byrsinus discus*, *B. flavicornis*, *B. fossor*, *B. laeviceps*, *B. penicillatus*, *Geotomus elongatus*, *G. ciliatitylus*, *Microporus nigrita*, *Linospa candida*, *L. orbicularis*, *Exosehirus validus*. All of

these have characteristically oval, smooth and streamlined bodies to decrease resistance to movement within sand, and have elongated, toothed and densely setose front and rear legs to facilitate burrowing.

Heteroptera found around the bases of plants and around the roots include species of the family Pentatomidae: *Sciocoris deltacephalus*, *S. sulcatus*, *Putonia asiatica*, Scutelleridae: *Phimodera fumosa*, *P. bergi*, *Odontotarsus angustatus*, *O. impictus*, *O. obsoletus*, *Irochrotus lanatus*, *I. turanicus*, Coreidae: *Phyllomorpha lacerata*, Lygaeidae: *Emblethis denticollis*, *E. verbasci* *Blissus putoni*, and a large number of *Geocoris* species.

Sandy deserts had a large proportion of specialized feeders, reflecting the increased diversity of the sand desert flora. Oligophages, those restricted to feeding on one family of plants (Whitford, 2002) were most abundant feeding type, with 94 of the 152 species reported (61.8%). *Maurodactylus albidus* is an oligophage associated with crucifers, while grass associated species include *Ellipsocoris tamerlani*, *Odontotarsus angustatus*, *Odontotarsus impictus*, *Odontotarsus obsoletus*, and *Irochrotus turanicus*. Oligophage Heteroptera found in this study that are associated with trees and shrubs include *Atomoscelis onusta* (host *Salsola*), and *Atomophora alba* (host *Ammodendron*) and *Desertomenida albula* (host *Haloxylon*). Common predators include *Orius agilis*, *O. horvathi*, *Nabis palifer*, *Pasira basiptera*, and *Coranus subapterus*.

Other oligophage-host plant associations with ephemerals are: *Chlamydatus eurotia* and *Phytocoris turkestanicus* on teresken (*Ceratoides*), *Phyllomorpha lacerata* and *Cercinthinus annulipes* on *Salsola*, *Hyoidea noticeps* and *Dictyonota ephedrae* on *Ephedra*, *Atomophora pantherina* on *Calligonum*, and *Compsidolon pumilum*, *Tingis pusilla*, and *Stictopleurus abutilon* on *Artemesia*.

Many solonchaks are found within sandy deserts (Lioubimsteva, 2002) and support both solonchak and sandy desert vegetation and their associated Heteropteran fauna, especially where the ecotones separating the sandy desert from solonchaks are narrow. As in sandy deserts, the loose, sandy soils provides important subsurface habitat for arthropods. Solonchak deserts also have surface and ground water, albeit saline or alkaline, that can support specialized halophytic plant communities of salt tolerant shrubs, grasses and ephemerals in salt marshes, endorhetic river deltas, flood plains, river terraces and shores of saline lakes. Vegetation is divided into alkaline-saline and saline-shrub subgroups (Lioubimsteva, 2002). The characteristic Heteroptera of the solonchak include many desert endemic species that are closely associated with one or both of these two vegetation subgroups.

The first subgroup includes Heteroptera associated with *Anabasis salsa*, kokpek (*Atriplex cana* C.A.Mey.), kamforos (*Camphorosma monspeliaca* L.), and with plants of saline marshes and wetland, including *Suaeda* sp., *Limonium caspium* (Willd.) P. Fourn. and the saltwort *Sphaerophysa salsula* (Pall.) DC. Dominant Heteroptera species include *Henestaris halophilus*, *Pionosomus opacellus*, *Lamprodema maura*, *Sciocoris deltacephalus*, *Tarisa elevata*, *T. salsae*, *T. subspinosa*, and *Psallopsis Longicornis*.

The saline-shrub subgroup is associated with typical shrubs found in saline flood plains and along shores of saline lakes, such as *Halocnemum strobilaceum* M.Bieb. and species of *Tamarix*, *Halimodendron*, and *Eichinaphis*. Several of the dominant Heteroptera species are shared with the alkaline-saline group: *Tarisa elevata*, *T. salsae*, and *Engistus salinus*. Other common species are *Tarisa pallescens*, *Brachynema signatum*, *Desertomenida albula*, *Trigonotylus ruficornis*, *Artheneis alutacea*, *Nysius thymi*, *Agramma atricapillum*, and *Henestaris halophilus*. Common predators include *Nabis sinoferus*, *Orius agilis*, *O. albidipennis*, and *Pasira basiptera*.

The stony and clay desert types had the lowest numbers of Heteroptera species, genera and families, and the highest proportion of habitat generalist species. Both desert types lack suitable habitat and food resources, so Heteropteran abundances and species numbers are low. Two factors may contribute to this, the much reduced diversity and abundance of vegetation and nearly impenetrable surfaces. Clay and stony desert soils hold relatively little water, so the plant communities are much less diverse and productive than either the sandy or solonchak deserts, and vegetative cover is very limited and highly localized. Some soils in clay and stony deserts reduce infiltration to the extent that no perennial plants can survive (McAuliffe, 2000).

Whitford (2002) describes the factors that define vegetation in stony or gravel landscapes. The impervious surface of stony deserts prevents almost all infiltration, and rainfall runs off almost immediately. Vegetation is limited to runoff channels (runnels) and other depressions, where moisture and soil can accumulate. Gravel surfaces are almost impenetrable to root penetration, greatly limiting vegetation. Surface runnels accumulate wind or waterborne material. The type and abundance of vegetation found is a function of the depth of the channels and the amount of accumulated material. Shallow runnels can support only ephemeral plants, while deeper channels, where small channels merge, deeper soils may support perennial shrubs and desert grasses. The most common plants of stony deserts are lichens and mosses. The larger vegetation is limited to runoff channels and small depressions where both water and

wind and water borne debris accumulate.

The Heteropteran fauna is limited and closely associated with small elevation differences, where there is moisture and shrub vegetation. Heteroptera are found either on vegetation or in the debris immediately below the plants. A significant number of the stony desert Heteroptera are also found in the sandy, clay and solonchak deserts, with relatively few (20) specialized to this habitat, suggesting these more diverse habitats contribute much of the fauna of the stony desert.

Many are monophages or oligophages closely associated with specific plants, such as *Artemesia* sp., *Salsola* sp., *Salsola arbuscula* Pall., *Caragana* sp., *Anabasis* sp., *Nanophyton erinaceum* Bunge, *Atraphaxis* sp., and, *Ephedra* sp. The most commonly collected Heteroptera species were *Brachynema germari*, *Brachycarenum tigrinus*, *Tarisa elevata*, *Stictopleurus angustus*, and *Oxycarenum pallens*.

Clay deserts are dominated by extensive flat plains (takyr) which are filled with water during seasonal rains, interspersed with clay hills, plateaus and deep ravines. Clay desert soils with very high silts and clays soak up available moisture but once saturated, very little additional water can infiltrate and is lost as runoff. Seasonal rainfall collects in shallow lakes that rapidly evaporate. What moisture from rainfall is stored in the clay surface soils is rapidly lost to evaporation, supporting brief blooms of ephemeral vegetation after spring rains. Ground water in the clay desert lies deep, below the reach of roots of perennials.

The vegetation of the Kazakh clay deserts is composed of three types: spring ephemerals broadly distributed on the loess plains and intermountain valleys, highly localized xerophilic and halophilic shrubs and shrub-grass communities found in gullies and where the surface clays have been eroded. Desert sedges *Carex pachystylis* J.Gay, *C. enervis* C.A.Mey., *Poa bulbosa* L., and species of *Eremerus*, *Astragalus*, *Ferula* and other herbs are an important component of the ephemeral vegetation. A large number of Heteroptera from the clay deserts area associated with the ephemeral spring vegetation bloom, with the remainder associated with the xerophilic shrub vegetation in gullies and runnels. Species inhabiting the clay desert are primarily associated with species of *Artemesia*, *Ephedra*, *Ceratoides*, *Carex* and other halophytes. Only five species were found to be common. Of these, four were habitat generalists (*Brachycarenum tigrinus*, *Odontoscelis fuliginosa*, *Brachynema germari*, *Sciocoris deltacephalus*), and one (*Thologmus flavolineatus*) was also part of the sandy desert fauna.

The most characteristic clay desert Heteroptera species were monophages and narrow oligophages, such as *Atomoscelis onusta* and *A. alba*, and the 14 species of

*Tuponia* that were found almost exclusively in the clay desert. Other characteristic oligophages, such as *Aelia furcula*, were associated with grasses and sagebrush. Common predators include *Nabis palifer* and *Reduvius disciger*.

Habitat generalist Heteroptera, found in at least three of the four desert types, are eurytopic polyphagous xerophiles, with only a few oligophagous species. The polyphages are associated with *Artemesia*, *Atraphaxis*, legumes, and cereals, all broadly distributed plants found in all four desert types. Common generalist predators included *Nabis sinoferus*, *Holotrichius bergrothi*, and *Pasira basiptera*.

Desert arthropod species richness is dependent on the diversity and abundance of desert vegetation (Ayal et al., 2005; Floyd, 1996). Overall, it is the addition of specialist Heteroptera species that appears to be responsible for the greater species richness found in the sandy and solonchak deserts. These habitat specialists are either oligophages (or monophages) closely associated with characteristic sandy desert or solonchak vegetation, or are specialized species (Cydnidae) adapted to burrowing in loose, sandy soils. Conversely, the hard surfaced and vegetation poor habitats of the clay and stony deserts lack the habitat and food resources, resulting in a Heteropteran fauna dominated by polyphages and habitat generalist species.

Several previous studies suggest that the Palearctic desert Heteroptera of Central Asia may be highly diverse. Heteroptera are among the arthropod groups abundant in deserts, part of both canopy and ground dwelling fauna (Whitford, 2002). Kryzhanovsky (1965), working in the Irano-Turanian, and Central Asian deserts of the former USSR, reported that the Kazakh desert fauna included a large percentage of endemic insect taxa. Insect biodiversity is known to be high in Palearctic desert areas, with a large percentage of endemic taxa (Konstantinov et al., 2009).

Our findings of high species richness and high proportions of habitat specialists support these suggestions of high diversity in Central Asian Palearctic desert Heteroptera. In addition, the large number of species we found to be associated with only one of the four desert types, and the relative paucity of generalist species provides additional support for the contention that Kazakh deserts may support a large number of specialized endemic Heteroptera species. If Heteroptera are a good indicator group for overall arthropod diversity, as suggested by Duelli and Obriest (1998) and Ullrich (2001), then the presence of a species rich assemblage of Heteroptera, with many habitat specialized species, suggests that Kazakh deserts support high levels of arthropod diversity and endemism.

Overgrazing is a significant cause of habitat destruction

in the central and western deserts of Kazakhstan (Rachkovskaya and Bragina, 2012; Robinson, 2000). Tigar and Osborne (1997) found excessive grazing and disturbance by livestock and animal herders to lower arthropod numbers and diversity. Ayal and Merkl (1994) studied non-grazed enclosures and concluded that cattle grazing affected the relative abundance of tenebrionid species. In Kazakhstan, overgrazing has been reported to degrade sandy desert vegetation, changing community structure from the perennials *Aropyron fragile* (Roth) Dorn and *Artemisia* to annuals dominated by *Artemisia scoparia* Waldst. & Kitam. *A. leucodes* Schrenk. *Anisantha tectorum* (L.) Nevski, and *Ceratocarpus arenarius* L. (Rachkovskaya and Bragina, 2012, Robinson, 2000). This not only reduces the forage value of the vegetation (Robinson, 2000), it also affects the abundance of the diverse and endemic rich arthropod communities (MNRPE, 1999).

Energy development and road building, especially in the west of the republic, and unregulated irrigation and drainage are additional threats. Urbanization and intensive agricultural development of the foothills zone have damaged vegetative cover of the sandy deserts. The threat loss of arthropod biodiversity is real: "Kazakhstan's original ephemeroïdal and worm wood deserts have practically been destroyed" (MNRPE, 1999). This and other invertebrate biodiversity assessment research, now underway in Kazakhstan, will help planners and decision makers better manage national biodiversity priorities and bring additional protection to vulnerable arid land ecosystems.

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