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Diversity and community pattern of darkling beetles (Coleoptera: Tenebrionidae) along an ecological gradient in arid Mongolia¹

M. Pfeiffer & E. Bayannasan

Abstract

Three German-Mongolian entomological expeditions were conducted from 1997 to 2003 during summer in Mongolia. Tenebrionid beetles were sampled along transects from steppe to Gobi desert. For the 16 collection plots, we attained meteorological data from the Institute of Meteorology and Hydrology. We took notes of behavioral differences of the species and collected beetles from grain baits and with barber traps. At the 16 plots, we found from one to 12 species of Tenebrionidae. We examined 1688 individuals belonging to 38 species in total. *Anatolica* and *Blaps* were the dominant genera, with 11 and 10 species, respectively. Darkling beetle communities differed significantly in species composition in steppe, semi desert and desert. Certain species were highly dominant in certain plots in each of these habitats, e.g., *Scytosoma pygmaeum* in steppe, *Blaps femoralis* in semi desert, and *Anatolica potanini* in desert. Diversity pattern of tenebrionids was significantly influenced by climate conditions. Darkling beetle community structure as revealed by Nonmetric Multidimensional Scaling correlated with mean daily temperature and average monthly rainfall, as well as with plant community structure and plant diversity. Beta diversity of the plots was correlated to plot distance. Certain species of Tenebrionidae showed clear preferences for day and night activity.

Key words: Mongolia, German-Mongolian expedition, beetle, dominance, species diversity, community pattern

Introduction

One of the most conspicuous detrito- and phytodetritophagous groups of beetles in the Asian steppes and deserts is the family Tenebrionidae (Coleoptera, Polyphaga) (KONSTANTINOV et al. 2009). Mongolia harbors a rich diversity of these beetles with 215 species and 50 genera of Tenebrionidae listed for the country (MEDVEDEV 1990), many of them restricted to its arid parts, where they obtain high abundances and dominate – together with ants – the insect soil fauna (PFEIFFER et al. 2003). Their dark color may be a means to withstand the high radiation at daytime; however, a large number of species is night active and hide during the day in burrows or under sand. Some of the African species are known to be subsocial and even exhibit division of labor (RASA 1990), but information on the biology of the Asiatic species is scattered and rare. A lot of knowledge on the Tenebrionidae of Mongolia is based on the various expeditions of the famous Hungarian entomologist Dr. KASZAB, who was a taxonomic specialist for these beetles (KASZAB 1965, 1967, 1977). His research was continued by Medvedev (MEDVEDEV & KASZAB 1973, MEDVEDEV & LOBANOV 1990), who developed a key to the Mongolian Tenebrionidae (MEDVEDEV 1990), thus enabling further studies on the ecology of the species.

While the community ecology of darkling beetles has been studied in several arid regions of the world (STAPP 1997, BLAUM et al. 2009), especially in Israel (KRASNOV & SHENBROT 1996, 1998) and in the Mediterranean (FATTORINI 2006, 2010), little is known about the central Asian region. SAGDY (1996), investigated community pattern of Tenebrionidae in the Ubsunur Hollow Preserve in Tuva, but nothing is known on the ecological communities of the species rich Mongolian fauna.

¹ Results of the Mongolian-German Biological Expeditions since 1962, No. 318.

Our study aimed at a first assessment of tenebrionid communities in Mongolia along a northsouth gradient from steppe to desert. By carefully selecting plots for which meteorological data were available and a detailed study of plant diversity pattern at these locations, we obtained additional information on the environment of the beetle fauna. Our questions were in detail:

- 1) Which are the most abundant species of Tenebrionidae in the arid regions of Mongolia and which species have to be considered as rare?
- 2) Where is species diversity highest and which factors influence tenebrionid diversity pattern?
- 3) How are the darkling beetle communities structured and which factors influence the distribution of the species?
- 4) Moreover we assessed species' activity patterns to learn more about their niche preferences.

Study area and time

Mongolia lies in an ecological transition zone where the Central Asian Steppe meets the Siberian taiga forest and the Gobi desert. Located in the center of Asia, Mongolia has an extreme continental climate with very low precipitation, ranging from, e.g., 257 mm in Ulaanbaatar (UB, N 47° 56', O 106° 59') to 125 mm in Dalanzadgad (DG, N 43° 35', O 104° 25') and to less than 50 mm in the Transaltai Gobi. Most of the precipitation falls in summer. Temperature fluctuations are huge, both daily and annually. Absolute temperatures vary from -49°C in winter to + 40°C in summer. From North to South mean annual temperatures rise, e.g., from -1.1°C in UB to 4.3°C in DG.

This gradient of moisture and temperature in combination with different soil conditions and altitudinal changes results in a mosaic of different vegetation types (HILBIG 1995, HILBIG 2007): north of Ulaanbaatar vegetation consists of forest and mountain steppe, south of N 48° latitude a patchy steppe – semidesert (steppe-desert) – desert continuum extends up to the Chinese border (BRECKLE et al. 1994).

Generally vegetation zones in Mongolia correspond well with the distribution of precipitation (VON WEHRDEN & WESCHE 2007). In steppe zone short bunch grasses are dominant (LAVREN-KO & KARAMYSHEVA 1993). Semi-deserts are either dominated by *Stipa-Allium* communities (desert steppe) or by shrubs and dwarf shrubs (shrub desert steppes), e.g., *Artemisia, Cara-gana* (YUNATOV 1974). Desert zone vegetation is composed of low shrubs and semi-shrubs of the Chenopodiaceae, Tamaricaceae, Zygophyllaceae, Asteraceae, and others (PYANKOV et al. 2000). Vegetation cover there generally reaches values of less than 10 %, often only 1–2 % (WALTER et al. 1983). Very common in the desert steppe and desert are rodents, e.g. *Hemiechinus auritus, Meriones unguiculatus, Salpingotus crassicauda, Pygeretmus pumilio* and *Cardiocranius paradoxus* (STUERMER et al. 2004). Large herbivores, like Asian wild Ass (*Equus hemionus*), the Mongolian saiga (*Saiga tatarica mongolica*) and the Mongolian gazelle (*Procarpa gutturosa*) share the pastures with the livestock of nomadic herders (OLSON et al. 2001, KACZENSKY et al. 2008, BUUVEIBAATAR et al. 2009). Darkling beetles (Tenebrionidae) and ants (Formicidae) are dominant groups of the ground-dwelling insect fauna in these habitats (MEDVEDEV & LOBANOV 1990, PFEIFFER et al. 2003, 2006; PAKNIA et al. in print).

The main investigations of this study were done in two expeditions 1997 and 1999 to the south and east of Mongolia by a German-Mongolian team of scientists, who had a special focus on insect granivores, including darkling beetles and ants (PFEIFFER et al. 2003); a third expedition was conducted in 2003 during summer in south-west Mongolia (fig. 1).

Altogether 16 plots were sampled, which included three vegetation zones of Mongolia: desert, semi desert and steppe (table 1, fig. 2). The coordinates of these plots were determined by GPS (Garmin GPS 12 XL). Plots are listed here in the order of their recordings within the years:

1. **Maant.** A site of the dry steppe zone near to Ulaanbaatar dominated by *Artemisia adamsii*, *Leymus chinensis*, and *Carex duriuscula*. This plot was partly affected by nests of the common vole *Microtus brandti*.



- Fig. 1: A map of Mongolia. Given are the capital Ulaanbaatar, the routs of our expeditions and the positions of our study sites. The numbers indicate the following points in the order of sampling: 1) Maant, 2) Zorgol, 3) Choir, 4) Delgerekh, 5) Char Airag, 6) Saynshand, 7) Manlai, 8) Bayan-Zag, 9) Hongoryn Els, 10) Nemegt, 11) Ekhin Gol, 12) Tsogt testii 13) Grid 19, 14) Urtiyn ekh, 15) Ulapza robb, 16) Dulaan har uul.
- 2. **Zorgol.** At the foot of Zorgol Khayrkhan Mountain, this typical desert steppe plot was dominated by the peashrub *Caragana microphylla*, the Dzungarian bridlegrass *Cleistogenes squarrosa* and *Stipa krylovii*.
- 3. **Choir.** Desert steppe dominated by drought-resistant grasses *Cleistogenes squarrosa* and *Carex duriuscula*, and dwarf shrubs *Caragana microphylla*, *C. leucophloea*, and *C. steno-phylla*.
- 4. **Delgerekh.** This site was a meadow near a brook with more than 30 plant species, dominated by the Jiji grass *Achnatherum splendens*, Gobi feather grass *Stipa gobica*, and a *Kochia* species.
- 5. **Char Airag.** Desert steppe dominated by the caespitose grasses *Cleistogenes soongorica* and *Stipa glareosa*, and semi-shrub *Caragana pygmaea*.
- 6. **Saynshand.** A semi desert plot: the rocky slope of a hill dominated by *Cleistogenes soongorica*, *Allium mongolicum*, and gray sage bush *Artemisia xerophytica*.
- 7. **Manlai.** This place was heavily overgrazed when we visited it the second time in 1999. It was dominated by *Stipa glareosa*, and semi-shrubs of *Artemisia pectinata* and *Artemisia frigida*.
- Bayan-Zag. A saksa'ul (*Haloxylon ammodendron*) forest near Bulgan, co-dominated by Bassia dasyphylla and Setaria viridis partly with sandy dunes. The best examined plot of our study.
- 9. **Hongoryn Els**. This plot was a sandy place near the big dune of Hongoryn Els, about 1 km away from a small river. A mosaic of bare soil and densely covered hillocks, mainly with Nitre *Nitraria sibirica, Bassia dasyphylla*, and *H. ammodendron*.
- 10. **Nemegt.** A true desert plot in the Gobi Altai at the foot of Nemegt mountain. The rich flora of this site was dominated by *H. ammodendron* and the forbs *Artemisia caespitosa* and *Reaumuria soongorica*.

- 11. **Ekhin Gol.** A stony plot outside the oasis of Ekhin Gol that bore merely two plant species: *H. ammodendron* and *R. soongorica*.
- 12. Tsogt Stestii. An east Gobi plot with sparse vegetation.
- 13. Grid 19. The northernmost steppe plot, without plant recordings.
- 14. **Urtiyn Ekh**. An oasis with a small lake. We took samples in an adjacent population of saksa'ul (*Haloxylon ammodendron*).
- 15. **Ulapza robb.** A plot in the Sharga gobi. We sampled a dry river bed with sandy soils and many pebbles. There was a rich vegetation dominated by saksa'ul.
- 16. Dulaan har. A steppe plot with 25 % plant cover.



Fig. 2: Photographs of plot locations. From right to left, upper row: 1) Maant (Plot 1), 2) Zorgol (Plot 2); medium row: 3) Manlai (Plot 7), 4) Hongoryn Els (Plot 9); lower row: 5) Nemegt (Plot 10), 6) Ekhin Gol, (Plot 11).

Table 1: Research plots of the study, given are plot number (fig. 1), the locations, sorted from north to south, latitude, longitude, the corresponding botanical-geographical region, altitude, average rainfall, average temperature and mean maxima of daily air temperature, the Mar-tonne aridity index and total plant cover; for some of the plots not all data were available

plot number	location	geographical coordinates	botanical- geographical region (GRUBOV 1982)	altitude [m]	rainfall [mm]	mean daily temp [C°]	max daily temp [C°]	aridity index	total plant cover (%)
13	Grid 19	N 48°04.710' E 113°39.781'	Middle Khalkha	804	207	0.7	I	19.34	I
~	Maant	N 47°16.990' E 107°37.712'	Middle Khalkha	1571	196	-2.2	5.7	25.13	40
2	Zorgol Mountain	N 47°10.203' E 106°04.446'	Mongol. Dauria	1260	196	-2.2	5.7	25.13	53
16	Dulaan har uul	N 46°52.634 E 096° 36.945	"Many lakes"	2063	176	-1.64	5.03	21.05	25.3
က	Choir	N 46°21.535' E 108°17.309'	Middle Khalkha	1242	179	0.2	7	17.55	40
15	Ulapza robb	N 46°18.403 E 095°31.717	Ikh Nuur Depression	1187	76				14.6
4	Delgerekh	N 45°49.166' E 111°15.330'	Middle Khalkha	1048	197	1.4	8	17.28	43
5	Char Airag	N 45°37.812' E 109°30.323'	Middle Khalkha	1011	149	1.2	8.5	13.3	27
9	Saynshand	N 44°51.215' E 109°45.103'	East-Gobi	1003	112	3.7	10.7	8.18	30
1 4	Urtiyn ekh	N 44°48.632 E 097°22.084	Gobi-Altai	1355		ı	ı		28.4
œ	Bayan-Zag	N 44°10.456' E 103°42.165'	East-Gobi	1141	125	4.3	11.4	8.74	16
2	Manlai	N 44°04.618' E 106°44.068'	East-Gobi	1370	66	3.6	10.9	7.28	30
6	Hongoryn Els	N 43°46.478' E 102° 15.482'	Gobi-Altai	1360	125	4.3	11.4	8.74	56
12	Tsogt testii	N 43°43.087' E 105°48.913'	East-Gobi	1647	125,0	-	11.4	8.74	10
10	Nemegt	N 43°27.782' E 101°23.577'	Gobi-Altai	1327	84	4.96	11.4	5.61	21
5	Ekhin-gol	N 43°13.890' E 099°00.450'	Transaltai-Gobi	1032	115	9.24	11.4	5.98	15

Methods

Sample collection

In all of the plots sampled in 1997 and 1999 we placed 75 baited petri dishes in a 5 x 15 grid with approximately 5 m spacing. However, three additional plots, which were only sampled in 2003, were monitored with 35 barber traps and 40 baits. Petri dishes and barber traps were dug into the soil so that their edges were flush with the ground to allow easy access by darkling beetles. As bait we used a mixture of barley and millet seeds that were partly ground in a grain mill to produce a variety of particle sizes ranging from whole seeds to flour. We offered extra baits outside the plots: sugar water, cheese, and small pieces of meat. Baits were monitored every 2 h, beetles were removed from the baits and gathered in small buckets. Twice a day, shortly after sunrise and shortly before sunset, beetle samples were divided into morpho-species groups and counted. Counting and sampling of individuals at each plot took place at least for a full circle of diurnal and nocturnal surface temperatures. Surface temperature was measured hourly with Prima long digital thermometers. Air temperature and humidity were recorded with Hobo data loggers (Onset, ONS-H08-032-08). Because of the big size and the large number of beetles that comprised often more than one hundred individuals only a random chosen subset of each group was identified to species in the lab. Samples were stored in 70 % alcohol and brought to the lab of the Department of Ecology of NUM. Species identification was done with MEDVEDEV (1990).

Plant diversity within the grids was measured by plant cover estimates of all species. We included all vascular plant species, which were identified according to GUBANOV (1996) and GRUBOV (1982). On each location 10 squares were mapped. Single square size depended on the scale of the vegetation and was 1 m² in the steppe zone, 10 m² in semi-desert zone, and 20 m² in desert vegetation.

Analysis of diversity and community structure

From the collections a data matrix was generated which contained the plots as columns, while species and individuals gathered there were listed in rows. This matrix was used as a data input to the various computer software.

Calculation of alpha diversity for all plots and estimation of species richness was conducted with software EstimateS 8.2. (COLWELL 2010). We used the framework of JOST (2006) and converted diversity indices into "true" diversities, which represent the numbers of species in an evenly distributed population. The Morisita similarity index between darkling beetles communities of different plots was also calculated with program EstimateS 8.2. (COLWELL 2010).

We performed a multidimensional analysis of the community structure with PCORD 5.0. by Nonmetric Multidimensional Scaling analysis (NMDS). For analysis we pooled data for each plots and standardized it to equal sample size. Only species with at least three occurrences in all were included in the analysis to avoid accidental records biasing the results. Distances between the 16 plots were calculated with values of the first two NMDS axes. The NMDS extracts theoretical environmental gradients from the species composition data, thus monotonic relations between ordination axes and environmental parameters are to be expected (MCCUNE & MEFFORD 1999). Species scores are obtained with weight averaging. We used the Soerensen distance as a measure of dissimilarity of the plots, restricted the number of axis to 2, set the number of iterations to 250 and run PCORD with 1000 runs for real data and 249 runs with randomized data and the stability criterion fixed at 0.00001.

Impact of environmental parameters

Most plots were situated near to meteorological stations, and we took weather data of the Deutscher Wetterdienst and of local weather stations of the Mongolian Institute for Meteorology

and Hydrology to compare climatic variation of the plots. We used mean precipitation, mean daily air temperature and mean daily maxima, respectively, all calculated using data for the entire year. For each plot we calculated the De Martonne aridity index I = P/T+10, with P is annual precipitation [mm] and T = average annual temperature [C°].We also applied the mean plant cover of the plots as well as latitude and longitude.

NMDS scores and diversity measurements were correlated with the environment parameters to fathom the influence of the environment on the structure of the beetle communities. Correlation and regression analyses were restricted to the plots that were sampled in 1997 and 1999 with an identical sampling design and were computed with program STATISTICA 6.0 (STATSOFT 2001). For a first assessment of the correlation of plant community and beetle community structure, we performed a symmetric Procrustes rotation in R (function *protest* in package *vegan*, 5000 iterations) with the two NMDS (LEGENDRE & LEGENDRE 1998, OKSANEN et al. 2008, R Development Core Team 2012).

For comparison of beta diversity between the plots with plot distances, we read plot distances from the GIS measurements with Google Earth. Morisita similarity indices were converted to dissimilarities by subtracting them from 1 to allow processing with a mantel test, which was used to compare the resulting data matrices with a distance matrix of the localities and was calculated with vegan package 1.17-9 with 999 randomizations in R 2.11.1. (OKSANEN et al. 2008).

Results

We collected 1688 individuals and found 38 species of darkling beetles at the baits. At all 16 plots we found from 1 species (min.) to 12 species (max). *Anatolica*, with 11 species, and *Blaps*, with ten species, were the dominant genera at the 16 locations. Species abundances at all plots ranged from 243 to 1, with a median at 20.5 individuals, thus demonstrating a wide range from common to rare species (fig. 3). In each of the sites certain species of darkling beetles were highly dominant. For example *Scytosoma pygmaeum* dominated in steppe plot Zorgol Mountain (212 individuals), *Blaps femoralis* in semi desert at Sainshand (146 individuals) and *Anatolica potanini* in desert plots at Bajan Zag (141 individuals) (see Appendix 1). Plant communities of all plots consisted of a total of 91 species (data not shown) with between 3 and 25 species per plot.

Shannon diversity of beetle communities ranged from 1 to 6.66, while plant communities showed higher diversity and ranged from 1.47 to 7.71 for Shannon diversity; Simpson diversity was lower for both groups (table 2). Diversity measures of tenebrionids and plants showed no relationship, while Shannon and Simpson diversity of the beetles were correlated positively with temperature and negatively with rainfall (table 3). These results were corroborated by stepwise multiple regression analyses, which demonstrated that Shannon diversity of beetles was negatively influenced by rainfall (Beta = -0.67, adjusted R² = 0.394; F_(1,10) = 8.14 p < 0.017, fig. 4a), while Simpson diversity was positively impacted by mean daily temperature (Beta = 0.65, adjusted R² = 0.359, F_(1,10) = 7.17 p < 0.023, fig. 4b). At the same time Shannon diversity of plants reacted negatively to maximum daily temperature (Beta = -0.76, adjusted R² = 0.534, F_(1,10) = 13.62 p < 0.004), while Simpson diversity of plants was impacted negatively by mean daily temperature (Beta = -0.72, adjusted R² = 0.477, F_(1,10) = 11.02 p < 0.008).

Multivariate analysis of community pattern with NMDS clearly separated plots of steppe, semidesert and desert (final solution after 122 iterations, final stress: 19.688; Monte Carlo test for both axes with p < 0.001, fig. 5). As NMDS axes are identical for community scores (fig. 5a) and species scores (fig. 5b), they allow conclusions on the ecological niche of the different species. NMDS1 scores correlated significantly negatively with latitude, longitude, rainfall, aridity index and plant diversity, but positively with temperature; the second NMDS axis correlated negatively with maximum temperatures (table 3). As revealed by symmetric Procrustes rotation, NMDS axes



Fig. 3: Species abundance list for 33 species. Five species with mean abundances > 3, which could not be identified to species were excluded from the figure (see appendix for full data).



Fig. 4: Results of regression analyses show the impact of environmental factors on tenebrionid diversity pattern. 4 a) Impact of rainfall on Shannon diversity of Tenebrionidae. 4b) Simpson diversity was impacted by mean daily temperature.

of beetle community and plant community correlated strongly (R-function *protest*, 5000 permutations, r = 0.7307, $r^2 = 0.53$, p = 0.0012).

Beta diversity of the plots was correlated to plot distance as calculated with the inverted Morisita similarity index (Mantel correlation with (1-Morisita index) n = 128, r = 0.281, p = 0.006), thus demonstrating that dissimilarity of beetle communities rose with the distance between them.

Table 2: Beetle abundance and diversity measures D⁰, D¹ and D² according to JOST (2006) for the communities of darkling beetles and plants in our plots, listed from north to south. Given is species richness, Shannon diversity and Simpson diversity, the latter both "true diversities" not indices (JOST 2006)

		Teneb	orionidae			plants	
	abun- dance	species numbers	Shannon diversity	Simpson diversity	species number	Shannon diversity	Simpson diversity
Grid 19	12	2	2	2	-	-	-
Maant	26	4	3.07	2.70	25	7.71	5.24
Zorgol	281	5	2.21	1.67	11	6.31	5.09
Dulaan har uul	189	9	6.66	5.59	14	6.83	5.11
Choir	13	1	1.00	1.00	21	5.64	3.72
Ulapza robb	65	5	3.73	3.11	5	2.33	1.78
Delgerekh	21	3	1.65	1.34	17	4.38	2.26
Char Airag	81	4	2.83	2.32	18	5.76	4.25
Saynshand	264	12	5.62	4.29	19	5.40	3.15
Urtiyn ekh	157	7	3.21	2.46	12	5.39	3.64
Bayan-Zag	319	12	4.14	3.04	10	4.61	3.41
Manlai	20	5	4.41	4.08	12	3.05	2.43
Hongoryn Els	129	7	2.92	2.78	5	1.47	1.21
Tsogt testii	12	3	2.75	2.57	9	3.28	2.09
Nemegt	49	8	3.24	2.09	15	5.66	3.93
Ekhin-gol	44	7	5.48	4.77	3	1.99	1.99

Table 3: Results of Pearson correlations of abundance, species richness and diversity of beetles, as well as NMDS scores with environmental and biological parameters

			Tenebr	ionidae		
	abun- dance	species numbers	Shannon diversity	Simpson diversity	NMDS1	NMDS2
Latitude	-0.015	-0.52	-0.58*	-0.55*	-0.86***	0.14
Longitude	-0.015	-0.52	-0.58*	-0.55*	-0.86***	0.14
Altitude	0.405	-0.13	-0.09	-0.04	0.08	0.48
Rainfall	-0.006	-0.62	-0.69**	-0.63*	-0.81***	0.22
Mean Daily Temperature	-0.014	0.49	0.66*	0.66*	0.70**	-0.41
Max Daily Temperature	-0.010	0.56	0.60*	0.59*	0.87***	-0.67*
Aridity Index	0.073	-0.55	-0.63*	-0.60*	-0.83***	0.34
Total plant cover (%)	0.011	-0.27	-0.49	-0.43	-0.43	0.19
Plants species number	0.011	-0.20	-0.26	-0.30	-0.65**	0.43
Shannon diversity plants	0.244	0.02	-0.06	-0.16	-0.63*	0.36
Simpson diversity plants	0.259	0.05	0.03	-0.06	-0.59*	0.31

significant correlations are printed in bold and marked with stars p < 0.001 = ***, P < 0.01 = ** and p < 0.05 = *



Fig. 5: a – Plot scores of the multiple community analysis with NMS. Plots of desert, semi-desert and steppe were clearly separated by the two NMS axes. b – Species scores of the multiple community analysis with NMS given in fig. 5a. The coordinates are equal to fig. 5a.

Following species are represented by the numbers: 1 = A1, 2 = A2, 3 = Anatolica amoenula, 4 = Anatolica cellicola, 5 = Anatolica "femoralis", 6 = Anatolica grebenscikovi, 7 = Anatolica mucronata, 8 = Anatolica nureti, 9 = Anatolica polita, 10 = Anatolica potanini, 11 = Anatolica psendaucta, 12 = Anatolica sternalis, 13 = Anatolica undulata, 14 = Blaps acuminata, 15 = Blaps femoralis, 16 = Blaps femoralis medusula, 17 = Blaps kiritshenkoi, 18 = Blaps kowhagarensis, 19 = Blaps medusa, 20 = Blaps militaris, 21 = Blaps reflexa, 22 = Blaps rugosa, 23 = Blaps sp. 1, 24 = Blaps variolosa, 25 = Cyphogenia chinensis, 26 = Eumylada punctifera, 27 = Melanesthes ciliata, 28 = Melanesthes maxima, 29 = Melaxumia angulosa, 30 = Microdera kraatzi, 31 = Monatrum prescotti, 32 = Platyscelis brevis, 33 = Scytosoma pygmaeum, 34 = Sternoplax zichyi, 35 = T1, 36 = T10, 37 = T3, 38 = Trigonoscelis sublaevigata.

Further ecological data on niche dimensions could be obtained from the sampling time of the beetles. Certain species of Tenebrionidae showed clear preferences for day and night activity (fig. 6).



Fig. 6: Day and night activity of the most abundant darkling species in percentages of 24 hours. Most of the observed species were night active. The number of observations is given in brackets after the species names *Trigonoscelis sublaevigata* (16), *Melanesthes maxima* (7), *Emylada punctifera* (13), *Blaps medusa* (45), *Blaps kowhagarensis* (7), *Blaps reflexa* (16), *Anatolica cellicola* (4), *Scytosoma pygmaeum* (448), *Microdera kraatzi* (475), *Blaps femoralis* (238), *Anatolica amoenula* (26), *Sternoplax zichyi* (67), *Anatolica nureti* (109), *Cyphogenia chinensis* (31), *Blaps rugosa* (93), *Anatolica sternalis* (79), *Anatolica potanini* (358), *Anatolica polita* (16), *Melaxumion angulosa* (6), *Blaps kiritschenkoi* (23), *Anatolica undulata* (16).

Discussion

Compared to the 215 species of Tenebrionidae that are listed for Mongolia (MEDVEDEV 1990), our standardized collection included only a small part of the country's whole tenebrionid diversity, although sampling effort was high and we compared 16 plots in widely differing habitats. Interestingly a lot of the species have been rare (8 species were collected only once), while others were dominating their plots in higher numbers. Moreover, 17 species were found in only one of the plots, thus pointing towards a high ecological specialization of these species. Diversity of beetles, as measured with different measures, was negatively influenced by rainfall and positively impacted by mean daily temperature, thus following a gradient from steppe to desert with higher diversity in the South. Community pattern, but not diversity, of the Tenebrionidae was highly correlated to plant diversity and plant community structure and was also influenced by climate factors, thus corroborating the ecological adaptation of these Coleoptera.

As environmental factors have a high impact on species communities it is not surprising that species identity in our samples was quite different from those species found in a study of darkling beetles in the Russian Ubsunur Hollow steppe in Tuva examined by SAGDY (1996). This is in line with our results on beta diversity, which clearly show that species similarity of plots declined with rising distance between them. The darkling beetle community structure in Sidunzi of Yanchi, Ningxia, China, (YANG et al. 2010) seemed to be more similar to those in Mongolia, as it was dominated by *Blaps femoralis* and *Microdera kraatzi* (fig. 7) two species that were also abundant in our plots. Our results corroborate the findings of these authors that the darkling beetles had different demands for multidimensional ecological resources in desert and semi-desert ecosystems.



KRASNOV & SHENBROD (1996), who studied species' microhabitats, have stressed the soil structure as a potential further environmental factor to separate darkling beetles communities, which was not covered in our study and should be included in further research on the taxa. Similarly YANG et al. (2010) underline the importance of soil water content.

Our data on darkling beetles' activity pattern are unique and shed some light on the life history of Asian Tenebrionidae, for which not many data exist. However, as results from American shortgrass prairie show, activity pattern of tenebrionid species may vary in different habitats and at different times (STAPP 1997). More studies on the life history of the Mongolian Tenebrionidae are urgently needed to fully understand the biology of these beautiful species.

Fig. 7: *Microdera kraatzii*, a tenebrionids beetle species with an uncommon body shape, was dominant in many desert plots.

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Appendix: Abundances of Tenebrionidae at the different study plots

Zorgol Mountain	0	0	0	0	0	0	0	0	0	0	0	0	6	0	ო	0	0	0	0	0
Urtiyn ekh Oase	0	0	0	0	0	0	0	0	10	0	0	0	0	87	ю	0	0	0	e	0
Ulapza robb	0	0	0	0	4	19	0	0	0	0	0	0	0	8	30	0	0	0	0	0
iitsət testii	0	0	2	4	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0
bnshanys2	-	-	-	0	0	0	0	27	0	22	0	58	0	0	102	0	0	0	0	-
tgəməN	0	0	0	0	0	0	0	33	9	4	0	0	0	0	0	~	0	0	0	0
isInsM	0	0	7	0	0	0	0	4	0	4	0	0	0	0	4	0	0	0	0	0
tnseM	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0
Els Hongoryn	0	0	0	0	0	0	0	5	0	72	0	7	0	0	0	0	23	0	0	0
Grid 19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iog-nida∃	0	0	0	0	0	0	0	6	13	0	0	0	0	0	e	0	0	4	0	0
Dulaan har Uulaan har	0	0	0	19	0	56	0	0	0	0	34	0	30	œ	0	0	0	0	0	0
Delgerekh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	~	0	0	0	0	0
Choir	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Char Airag	0	0	с	0	0	0	0	0	0	0	0	14	0	0	15	0	0	0	0	0
geZ-neveB	0	0	5	0	0	0	з	-	0	141	0	0	0	0	2	0	0	0	23	0
	A1	A2	Anatolica amoenula	Anatolica cellicola	Anatolica sp. "femoralis"	Anatolica grebenscikovi	Anatolica mucronata	Anatolica nureti	Anatolica polita	Anatolica potanini	Anatolica psendaucta	Anatolica sternalis	Anatolica undulata	Blaps acuminata	Blaps femoralis	Blaps femoralis medusula	Blaps kiritshenkoi	Blaps kowhagarensis	Blaps medusa	Blaps militaris

B Appendix: Table continued

BsZ-nsya	Char Airag Choir	Delgerekh	Dulaan har Dulaan har	Iog-nid≯∃	Grid 19	Els Hongoryn	aant Maant	isInsM	1gəməN	bnshanys2	Tsogt testii	Ulapza robb	Urtiyn ekh Oase	Zorgol Mountain
0	0	0	∞	0	0	0	0	0	0	0	0	0	0	7
0	0	0	26	0	0	0	0	0	0	12	0	0	0	46
0	0	0	0	0	0	0	0	0	0	0	0	0	48	0
0	0	0	4	~	0	0	0	~	0	0	0	0	0	0
0	0	0	0	0	0	10	0	0	2	0	0	4	3	0
0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
0		0	0	0	9	0	0	0	0	0	0	0	0	0
49 (\sim	18	4	3	0	2	0	0	1	33	0	0	3	0
0		0	0	0	0	0	0	0	0	2	0	0	0	0
0		0	0	0	0	0	-	0	0	0	0	0	0	0
0 1	З	2	0	0	0	0	4	0	0	0	0	0	0	212
0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	9	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	11	0	0	0	0	0	0	0	0	0	0
81	က	21	189	44	12	129	26	20	49	264	12	65	157	281