# Ground-beetle communities in the Lake Elton region, southern Russia: a case study of a local fauna (Coleoptera: Carabidae)

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## ABSTRACT

In principle, full-scale seasonal catches with the use of various sampling techniques appear to adequately reflect any local fauna of ground-beetles. Considering the differences in abundance and demographic structure of the populations, three groups of species in any fauna of Carabidae can be distinguished: residents, migrants and casual, or sporadic, species. Residents are characterized by a complete demographic structure of their populations while their habitats are considered as "residential". In migrants and sporadic species, the demographic structure is incomplete while their habitats are considered as "transit". Both latter groups combined can be termed as "labile components of the fauna", as opposed to "stable components of the fauna" represented by residents. During a fullyear survey in 2006/07 in the Lake Elton region, Volgograd Area, Russia, 218 species of ground-beetles were recorded. In zonal habitats, residents play the leading roles and form the main component of the assemblage. More than 65% of the total abundance and up to 35% of the total species diversity comprises of residential species. In azonal habitats, the labile component absolutely prevails. These species account for about 94% of species composition and about 75% of abundance. Thus, from a methodological viewpoint, it is highly important to distinguish between these two components of the fauna in any ecological studies of Carabidae. The Margalef index, one of the possible measures of $\alpha$-diversity, shows an expectedly strong dependence on the completeness of species lists, in some cases with 30-fold differences in values noted. In contrast, both

Shannon-Wiener's diversity index and the Berger-Parker dominance index, two further measures for α-diversity determination, scale must better, with the difference in values for complete and incomplete species lists ranging from 2% to 75%. Jaccard's coefficient of community similarity, as well as the Czekanowsky-Sørensen similarity index, both measures of β-diversity, depend on the way of calculation and of the count of labile components, especially for intrazonal habitats. Species compositions which are highly variable in space and time substantially reduce the availability of faunistic checklists based on standard collecting methods for geozoological and zoogeographical analyses. Studies on the demographic structure of individual species' populations are highly important for the revelation of faunas both of separate habitats and the landscape as a whole. To improve the reliability of faunistic species lists, the following can be proposed: (1) reduction to one season of the study period, but with an increased intensity and variety of collecting techniques used; and (2) reduction the scope of the model study group to taxa with more or less uniform migratory capacities and other ecological parameters.

## INTRODUCTION

As a rule, in zoological studies the term "concrete (= local) fauna" (Chernov, 1975, 1984) is used as a direct analogue to the term "concrete flora" (Tolmachev, 1931). It is thereby believed that a competent zoologist can evaluate the species composition of a study animal group the same way as a botanist that of vascular plants. However, the obvious difficulties in the identification of numerous animal taxa disturb this analogy. Thus, the local fauna concept is then somewhat restricted, because practical studies are based on individual, more or less large groups. Such a taxonomic specialization is clearly observed in entomology. In entomological investigations, local fauna approaches usually concern the family or even generic level. As regards carabid beetles, both of them have been used in various faunistic and zoogeographical studies (Penev & Turin, 1994; Penev, 1996; Voronin, 1999; Kozyrev et al., 2000).

Besides difficulties in the identification of species, there are several additional problems: (a) based on different collecting techniques, species lists can vary; (b) the efficiency of the same collecting methods can differ considerably depending on habitat; (c) since different developmental stages of insects are captured in various proportions or numbers, the determination of the species composition strongly depends on the phenological conditions of the population. These issues lead to serious biases in sampling and analysis (Kudrin, 1966; Arnoldi et al., 1972; Luff, 1975; Adis, 1979; Ericson, 1979; Gryuntal, 1982; Matalin, 1996; Markgraf & Basedow, 2000; Esch et al., 2008; Timm et al., 2008). Thus, the efficiency of pitfall trapping, a technique appropriate for the sampling of a mobile part of the carabid population, appears to depend on trap size

(Waage, 1985), trap setting (Greenslade, 1964; Korczyński & Sienkiewicz, 2006), the presence or absence of a fixative (Karpova & Matalin, 1992), as well as the type of fixative used (Luff, 1968; Feoktistov, 1980; Gryuntal, 1982). Furthermore, the mobility of beetles changes during the season and clearly depends on their physiological condition and on abiotic environmental factors.

Immobile or poorly vagile stages, such as eggs, larvae and pupae, are usually collected in soil samples or with the use of some other sampling techniques like flotation, Berlese funnels etc. These methods are also characterized by their own respective biases which depend on sample area or volume, the selection of sampling plots, frequency of sampling, etc. (Arnoldi et al., 1972; Boháč, 1973; Desender & Segers, 1985).

In addition to these issues, there are two further problems. Firstly, many Carabidae (phytobionts, troglobionts, myrmecophiles etc.) can only be captured using specific sampling methods (Paarmann & Stork, 1987). Secondly, in some habitats, the use of several collection techniques at once appears to be restricted or even impossible. Thus, stony tundra habitats would not allow quadrat soil sampling. Nor would it make sense to apply light trapping in high latitudes or altitudes.

Some of the biases concerning the imperfection or selectivity of different sampling methods could be avoided, albeit hardly entirely eliminated, by trapping protocol standardization, an increased number of traps or samples, the use of geostatistical methods etc.

The main objectives of the present paper lie in a study of the local fauna, or faunule, of Carabidae of the Lake Elton region, southern Russia, as well as in an evaluation of the efficiency of species composition determination.


## MATERIAL AND METHODS

In 2006-2007, ground-beetle communities in the Lake Elton region, Volgograd Area, Russia, were studied. The area is located near the Russian-Kazakhstan frontier (49°12.47'N, 46°39.75'E). The demographic structure of the populations of relatively abundant species was the main task of our work. As additional objectives, the species composition in the different habitats, as well as the between-habitat distribution of some species were considered.

Lake Elton is situated inside the blind drainage Botkul-Bulukhta Desert Depression, which belongs to the Caspian Lowland. A strongly pronounced salt-dome structure is characteristic of this region. The largest salt-domes are placed on the eastern (Ulagan Mountain, altitude 68.0 m) and western (Presnyi Liman Hills, altitude 43.6 m) lakesides. The "axis" of the latest flexures is located between them. All of the rivers that disembogue into Lake Elton (four from the Northwest and three from the Southeast) flow along this "axis" (Nekrutkina, 2006). Against the background of a comparatively plain relief, the area supports flat ravines of different depth and extent. All these features cause a profound habitat mosaic. Because the Lake Elton region is situated at the borders between several natural-climatic zones, its landscape-zonal typology is still debated. According to some authors (Safronova, 2006),

this general area belongs to the steppe zone but, according to others (Sapanov & Gabdulin, 2006), to the semi-desert belt. Desert steppes are typical plant associations in most of the habitats there (Safronova, 2006). The most abundant plants in this landscape are *Artemisia lerchiana*, *A. pauciflora*, *A. austriaca*, *Kochia prostrata*, *Agropyron desertorum* and *Festuca valesiaca*. On salinas in floodplain terraces and in lakeside salt-marshes, hyper-halophilic communities are formed, where *Halocnemum strobilaceum*, *Atriplex cana*, *Anabasis salsa*, *Salicornia prostrata* (= *europaea*), *Salsola collina*, *S. tragus*, as well as *Artemisia santonicum*, *A. pauciflora*, *Suaeda physophora*, *Limonium suffruticosum*, *L. caspium* and *L. gmelinii* are dominants. Dense reedbeds occur in the river valleys, while in gullies on lakesides there are trees and shrubs. Near the village of Elton, all desert steppes are broke or transformed into pastures. At present some of these are developed into fallow lands of different ages.

On the whole, the diversity of landscapes in the Lake Elton region is rather low, thus making the problem of determination of carabids much simpler. Because of long-term investigations (Kalyuzhnaya et al., 2000; Komarov, 2002), the fauna of ground-beetles of this area is well-studied. Therefore, we have a good chance to compare the efficiency of intense, year-round studies with regular trapping over many years, but using data from short trapping periods.

During both years of this survey, beetles were collected in six zonal, one exclave and three intrazonal habitats[*] (Table 1, Figs 1-2). Three of these were located near the village of Elton, while seven were located on the northwestern shore of Lake Elton, on the right bank of the Khara River (Fig. 3).

Three basic methods were used for collecting the beetles: pitfall traps, a light trap and different hand trapping methods.

Plastic pitfall traps of 0.5 l capacity and 95 mm upper diameter containing 4% formalin as a fixative were used. In each habitat, the traps were arranged along a transect at 10 m intervals. Because of the high daily air temperature and low air humidity, the fixative content was increased to 3/4 of the trap's volume. The traps were set from 10 May 2006 until 10 May 2007 and were checked at 10-day intervals on the 10th, 20th and 30th (31st) of each month. The traps were maintained rom November 1st, 2006 until March 31st, 2007.

The light trap, fitted with an 8-watt ultraviolet lamp, was used at the village of Elton from 18 May until 31 September 2007. It was emptied each morning, except between 23 and 29 July, and between 14 and 19 September.

Hand catches, using entomological sweep-netting and soil samples, were taken occasionally various locations in the Lake Elton region (Fig. 3).

Generally, the arrangement of the sampling plots corresponded well to small (environs of Elton Village) and mid-sized (Lake Elton region as a whole) samples, according to Yurtsev (1975). Using Penev's (1996) criteria, the study habitats actually belonged to two local faunas, one from the western (lower reach of the Khara River), and the other from the eastern (environs of Elton Village) part of the region (Fig. 3).

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[*] The division of plant associations into zonal, exclave and intrazonal is given according to Chernov (1975). Both exclave and intrazonal habitats are recognized here as azonal.

**Table 1.** Study habitats in the Lake Elton region.

| Codes | Habitats | Locations | Coordinates |
|---|---|---|---|
| **Zonal communities** | | | |
| Zs_ds | Sagebrush desert steppe | Left bank of Bol'shaya Smorogda River, "Otgonnyi" | 49°06.74'N 46°52.64'E |
| Zsg_ds1 | Sagebrush-grassland desert steppe | | 49°06.71'N 46°52.62'E |
| Zsg_ds2 | Sagebrush-grassland desert steppe | Northern slope of Ulagan Mountain | 49°12.71'N 46°39.83'E |
| Zgf_s | Grass-forb steppe | Slope of floodplain terraces on the right bank of Khara River, 4 km upstream of mouth | 49°12.91'N 46°40.03'E |
| Zsg_ds | Sagebrush-grassland desert steppe | Watershed of the Khara and Lantsug rivers, 4.5 km upstream of the mouth of Khara River | 49°13.33'N 46°39.75'E |
| Za_s | Grass-forb steppe with *Amygdalus nana* | Depression at the bottom of Khara River floodplain terrace, 3 km upstream of the mouth | 49°13.41'N 46°39.49'E |
| **Exclave communities** | | | |
| Ew | Riverine wood | Right bank of the Khara River, "Biological" Ravine | 49°13.69'N 46°39.18'E |
| **Intrazonal communities** | | | |
| Arb | Reedbeds | Floodplain section on the right bank of Khara River, 3 km upstream of the mouth | 49°12.87'N 46°39.72'E |
| Asl | Salina on floodplain terrace | | 49°12.39'N 46°39.78'E |
| Asm | Salt-marsh | Lakeside near the mouth of Khara River | 49°10.05'N 46°51.65'E |

Each specimen was dissected and the sex and age analyzed using a modified version of the method of Wallin (1987). On the basis of gonad condition, as well as mandibles, claws and cuticle, six physiological states in adults of both sexes were distinguished: (1) teneral; (2) immature; mature of either (3) the first or (4) second year of life; spent of either (5) the first or (6) second year of life. In addition, the degree of development of the hind wings and wing muscles was determined.

Seasonal changes in species assemblages were evaluated using the Wilson-Shmida measure for the chronological order of catches in each habitat:

$$I_{wc} = (g(H) + l(H))/2\alpha,$$

where $g(H)$ = number of species added with the next sample, $l(H)$ = number of species deleted with the next sample and $\alpha$ = average number of species for compared samples.

**Fig. 1.** Zonal habitats: A - sagebrush desert steppe at Otgonnyi; B - sagebrush-grassland desert steppe at Otgonnyi; C - sagebrush-grassland desert steppe on the northern slope of Ulagan Mountain; D - grass-forb steppe on the slope of floodplain terraces of Khara River; E - sagebrush-grassland desert steppe on the watershed of the Khara and Lantsug rivers; F - grass-forb steppe with *Amygdalus nana* in the depression at the bottom of Khara River floodplain terrace.

**Fig. 2.** Exclave (A) and intrazonal habitats (B-D): A - riverine wood in the "Biological" Ravine; B - reedbeds in the floodplain section of Khara River; C - salina on the floodplain terrace of Khara River; D - salt-marsh lakeside.
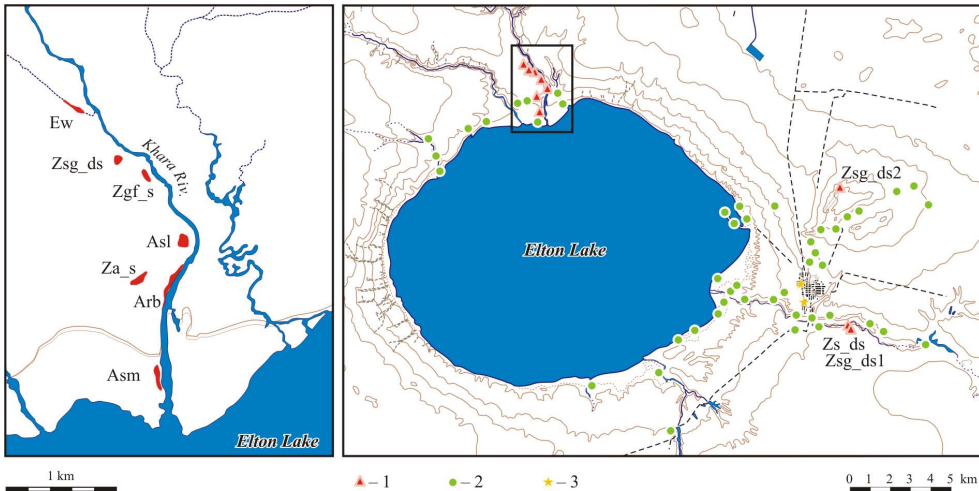


**Fig. 3.** Collection localities: 1 - lines of pitfall traps; 2 - locations of hand collection; 3 - light trap place and places of hand collection on light. The plot is shown on the right-hand side where, in the lower flow region of Khara River, seven lines of pitfall traps were set (after Google Maps).

Species lists were analyzed using the Margalef index of species diversity:

$D_{Mg} = (S–1)/\ln N$

as well as the Shannon-Wiener diversity index:

$H' = −\Sigma p_i \ln p_i$

and the Berger-Parker dominance index:

$d = N_{max}/N,$

where $S$ = number of shared species; $p_i$ = relative abundance of $i$-species ($n_i/N$); $N_{max}$ = number of specimens of more abundant species, $N$ = total number of specimens. Similarities between the faunas and populations in different habitats were estimated using Jaccard's coefficient of community similarity:

$I_j = c / (a+b-c),$

where $c$ = number of species shared by two compared habitats, $a$ and $b$ = number of species in the first and second habitats, respectively, as well as the Czekanowsky-Sørensen similarity index:

$I_{cs} = 2\Sigma \min(n_{ij}, n_{ik}) / (\Sigma n_{ij} + \Sigma n_{ik}),$

where $n_{ij}$ and $n_{ik}$ = numbers of species $i$ in habitats $j$ and $k$, respectively.

This was followed by clustering using the nearest-neighbor, distant-neighbor and unweighted mean methods. These calculations were made with "Biodiv 5.1" (Baev & Penev, 1995).

## RESULTS

During the period of observation, more than 52,000 specimens of Carabidae belonging to 218 species were collected. Our results correspond well with previous studies. According to the previous authors, the Lake Elton region supports 243 species of Carabidae. However, 20% of our species list differs from theirs (Kalyuzhnaya et al., 2000; Komarov, 2002). Thus, 43 species are recorded from this area for the first time. Among these, three species are new to the fauna of the Volgograd Area, while further two are new to the Russian fauna. On the other hand, 51 species previously reported from the Lake Elton region were not detected in this study. Therefore, based on the data obtained, we can conclude that full-scale seasonal catches with the use of various sampling techniques adequately reflect the local fauna.

It is noteworthy that a considerable component of our species list (103 species) appears to consist of singletons , represented by only one method of collection. Thus, 29 species were trapped only by light, 11 taken only by hand, while a further 63 occurred only in pitfall traps. Thereby, pitfall traps yielded mainly trivial species in zonal habitats.

Most of the unique records belonged to intrazonal habitats, with 4-6 records per trapping line per season.

A comparative analysis of the species accumulation curves (Fig. 4) for the different habitats shows that relatively long-term studies are necessary to adequately reveal the species composition. Concerning the zonal habitats, a basic species list can be created even after the first two months of trapping. In intrazonal habitats, however, there is a visible increase in species diversity over virtually the whole period of trapping. Some species were recorded only at the beginning or towards the end of the season.

Whilst the accumulation curves well characterize the representativeness of this study of the fauna, they fail to describe the seasonal variability of the species composition. This was done using the Wilson-Shmida measure, calculated step by step for the adjacent trapping periods. In all the studied habitats, this index was found to change from 0.15 to 0.95, but the pattern of changes varied. In some cases (*Za_s* and *Zsg_ds2*), a period of rapid change (10-20 days) in species composition was observed in the spring and early summer, while in the others (*Ew*) it occurred in the autumn. Most often, the Wilson-Shmida's measure showed a bi- or polymodal pattern (Fig. 5). Interestingly, the intensity of change in species composition throughout the season in the zonal habitats with low species diversity levels was not lower, but even higher, as compared to the species-rich intrazonal habitats.
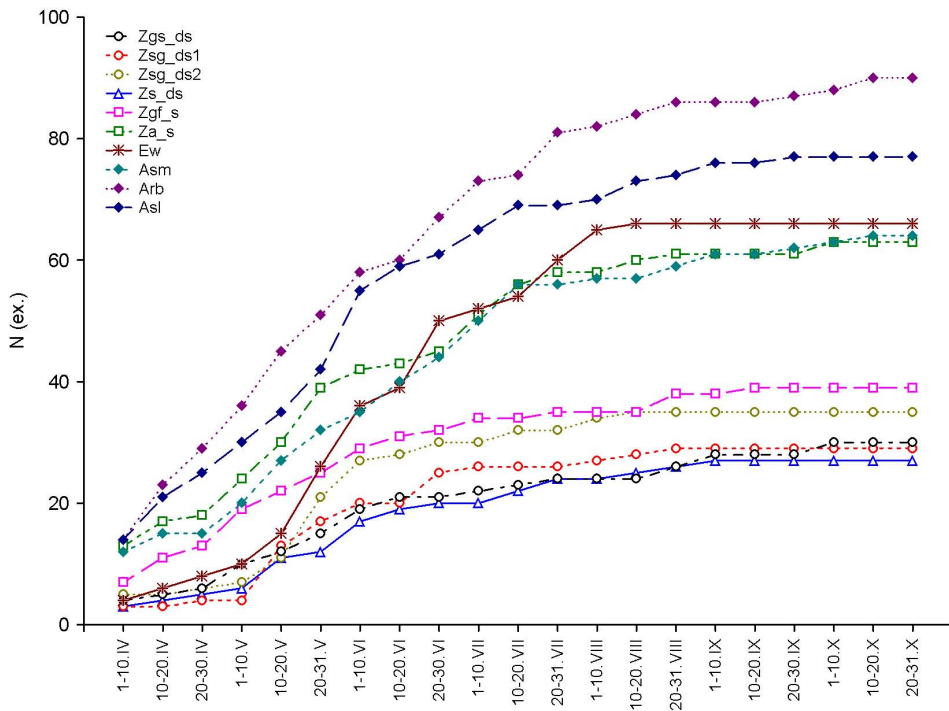


**Fig. 4.** Accumulation curves, showing the seasonal changes in the numbers of species in the studied habitats (abbreviations as in Table 1).
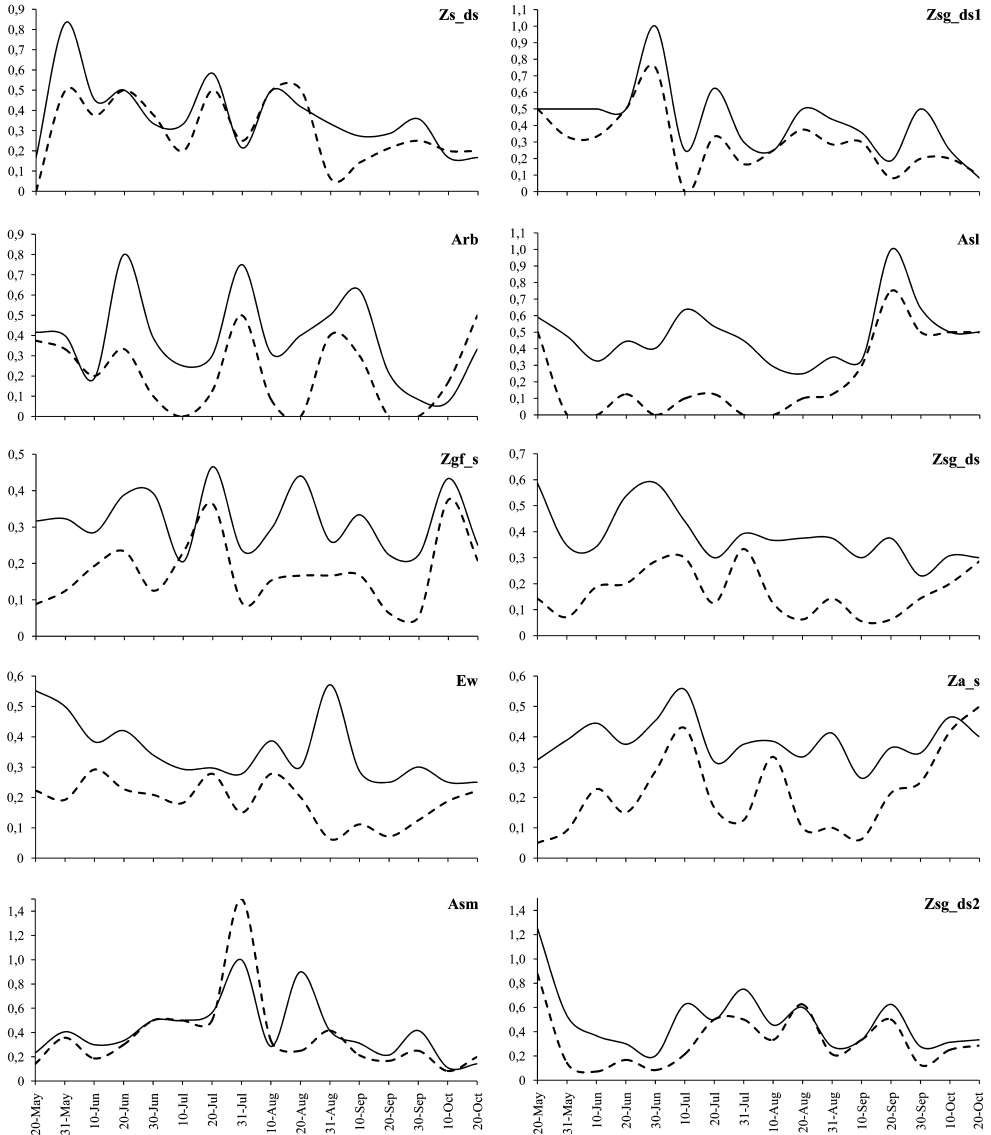
**Fig. 5.** Variation in the Wilson-Shmida measure for a chronological sequence of surveys at the study sites: solid line - a complete species list; dotted line - only resident (abbreviations as in Table 1).

Thus, a relatively complete picture of the species composition of Carabidae communities can only be attained by continuous counts with the use of different sampling methods throughout the whole season. Data obtained using a single collection technique over a short period or with large time gaps result in an incomplete representation of the

fauna. Similar conclusions have been obtained from a study of ground-beetle communities in Mediterranean habitats of Israel (Timm et al., 2008).

Changes in carabid community abundance and species composition can be due to both reproduction and redistribution of individual species. Usually this aspect is not considered in faunistic research. Because in our case the demographic structure of local populations was studied in due detail, these factors could be differentiated. Revealing the chronology and getting evidence of the maximum activity of beetles in different physiological conditions are of fundamental importance for such an analysis. This method does not demand quantitative counts of pre-imaginal stages, which is often difficult or virtually impossible, but it makes it possible to estimate the population condition using even relatively small samples (a few dozen specimens only).

In this study, the occurrence of individuals in a variety of physiological conditions is considered indicative of species which inhabit and breed in a particular habitat and not high abundance levels serve as a criterion of the successful existence and reproduction of a species' population in a particular habitat (e.g. *teneral → immature → mature → spent* for "autumn" or *immature → mature → spent → teneral → immature* for "spring" species), which is accompanied by clear peaks of catchability in the key points of the life cycle (as a result of feeding, reproduction or preparation for hibernation). The species which meet these demands (Figs 6-7) are considered here as "residents" and their habitats as "residential". An incomplete demographic spectrum of the population (Figs 8-9) or its lack in the corresponding periods of activity are evidence that a life cycle in this habitat is only realizable with low to zero probability. According to Bokhovko (2006), in the agricultural fields of the Kuban Region, southern Russia, incomplete life histories of Carabidae are observed in temporarily occupied habitats. Such species are considered here as "migrants" and their habitats as "transit" one.

In the Elton communities, only 76 of 218 species show high numbers at least in one of the habitats. Among these, only some 58 species (i.e. less than 1/4 of the total species list) are capable of completing their life cycles at least in one habitat (Table 2). Only one species, *Calathus ambiguus*, can be characterized as eurytopic, because it reproduces in nine of the ten studies habitats. About 3/4 of the species show only 1-2 residential habitats. The species which can reproduce in 3-4 habitats often reveal some selectivity, because they live either in zonal or intrazonal sites. Such biotopic preferences are shown in a small number (from four to 20) of residents per site. At the same time, from 28 to 93 carabid species were collected in a variety of habitats.

Therefore, when describing the fauna of each particular habitat, we must take into account that a considerable part of the species list is represented by migrants that are not restricted to that particular biotope. The role of migrants in creating a local carabid community remains open to question. The evident assumption concerning possible interactions, even mediate ones, between the migrants and residents, can be disputed by at least three arguments.

Firstly, even very high catchability levels of migrants in relatively small-sized habitats do not reflect the condition of the populations of other carabid species. Thus, in the
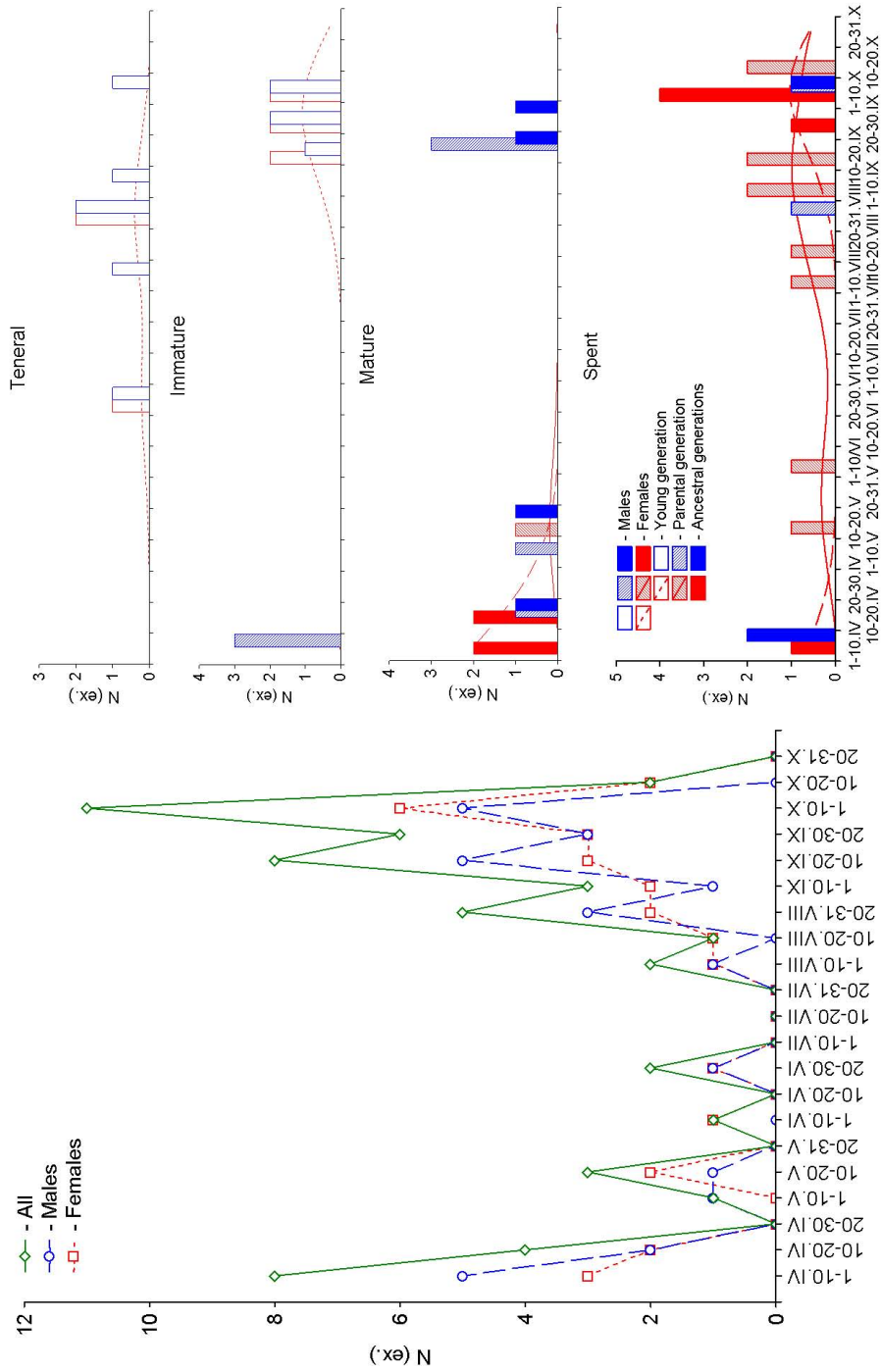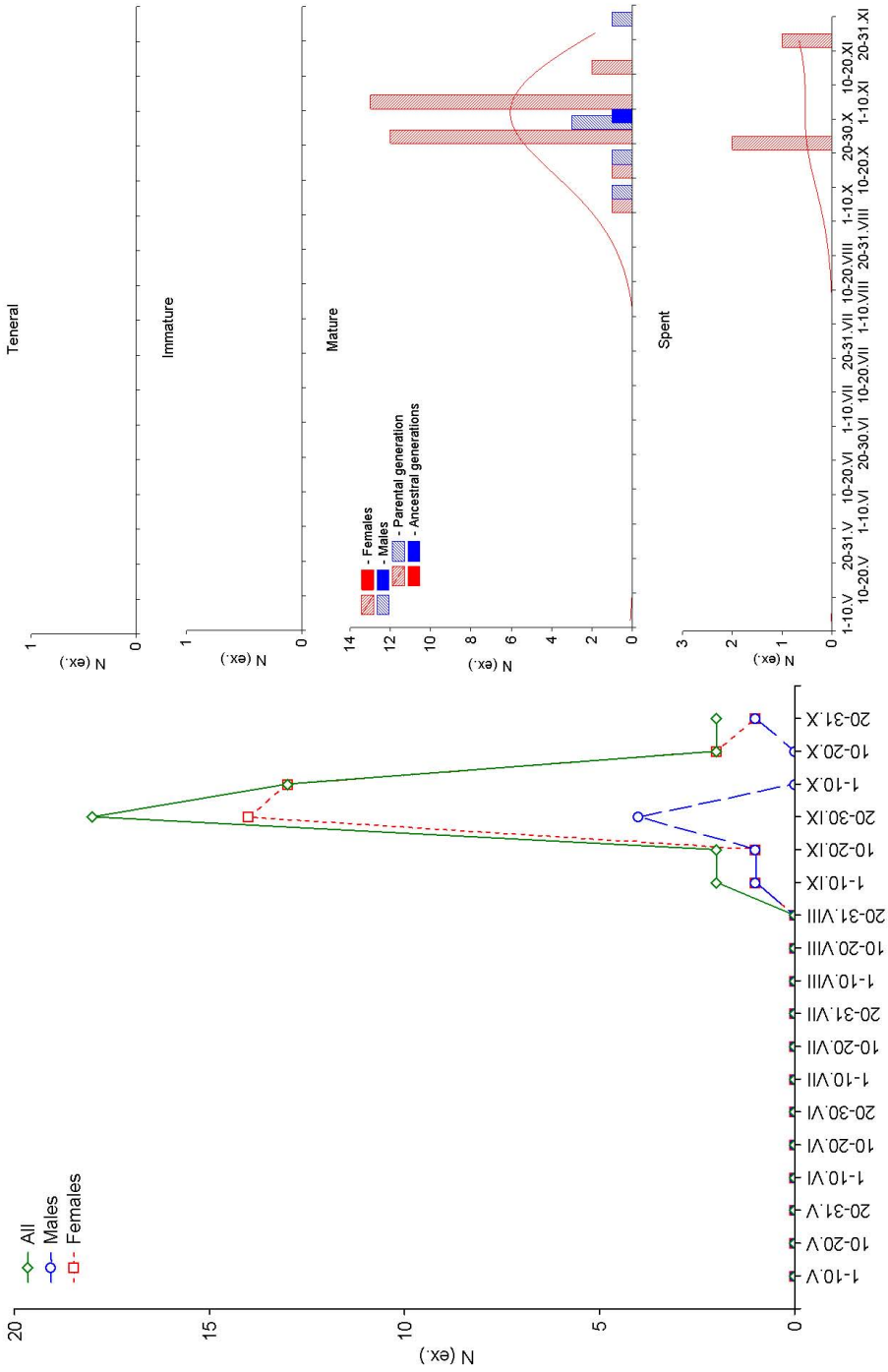
**Fig. 6.** Seasonal dynamics of activity, as well as the sex and age structure of the populations of *Carabus bessarabicus concretus* in grass-forb steppe with *Amygdalus nana* (combined data of 2006/07).
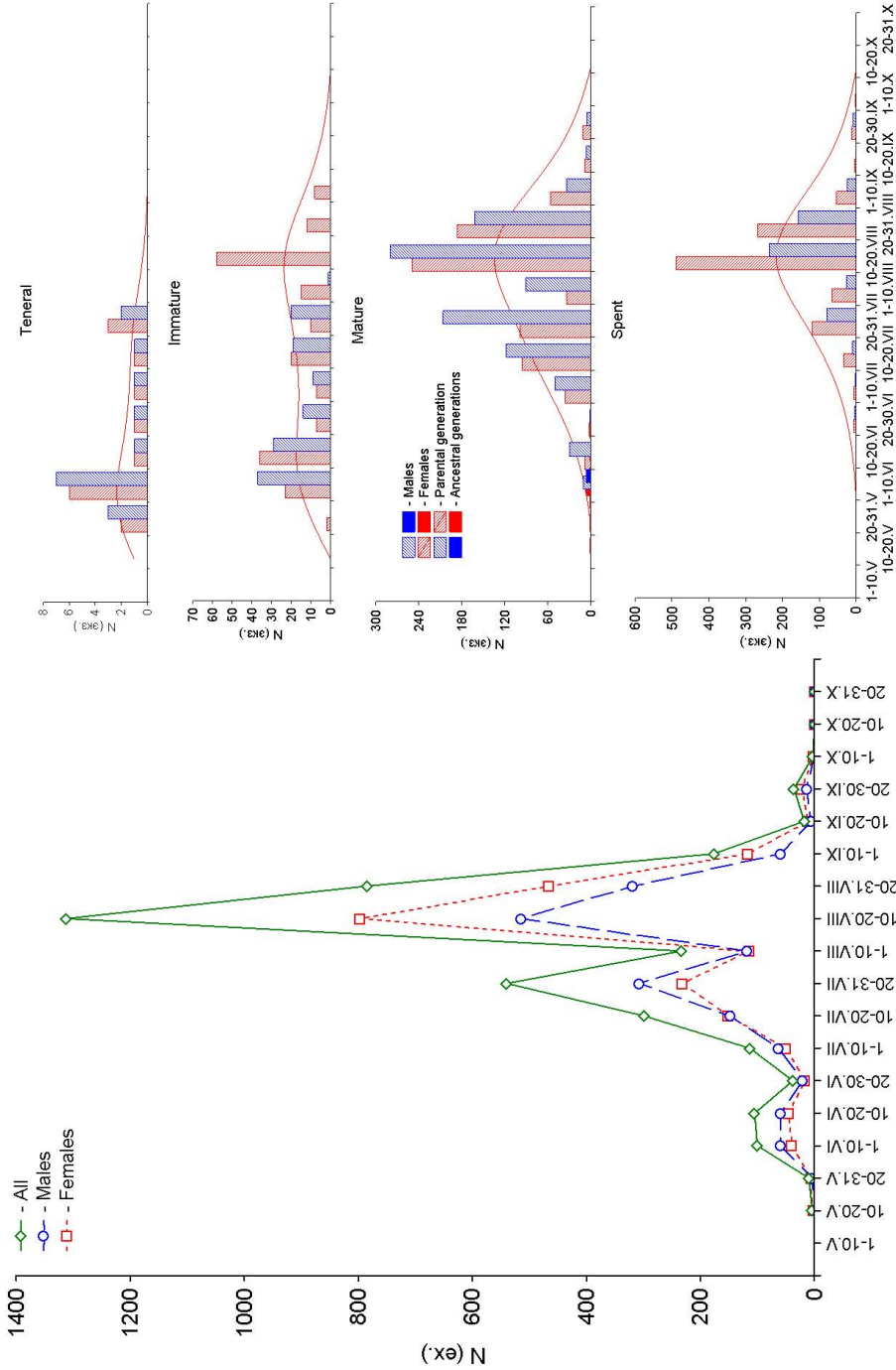
**Fig. 7.** Seasonal dynamics of activity, as well as the sex and age structure of the populations of *Cephalota elegans* from the lakeside salt-marsh (data of 2006).
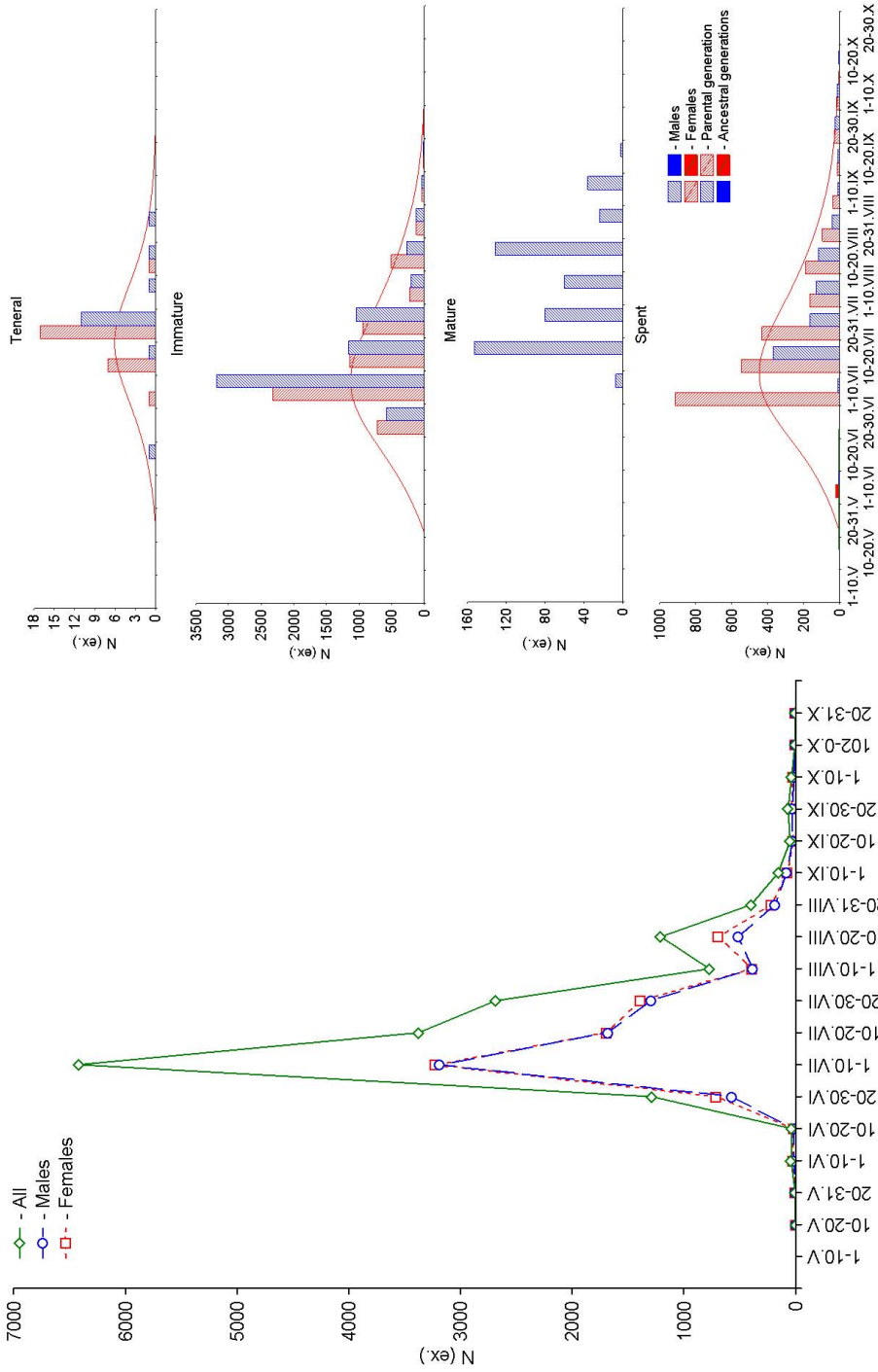
**Fig. 8.** Seasonal dynamics of activity, as well as the sex and age structure of the populations of *Harpalus rufipes* from the reedbeds (data of 2006).

**Fig. 9.** Seasonal dynamics of activity, as well as the sex and age structure of the populations of *Pseudotaphoxenus ruftarsis major* from the lakeside salt-marsh (data of 2006).

**Table 2.** Species composition and abundance of resident species of Carabidae in study habitats in the Lake Elton region.

| HABITATS / SPECIES | Zonal communities | | | | | | Exclave communities | Intrazonal communities | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Zs_ds | Zsg_ds1 | Zsg_ds2 | Za_s | Zgf_s | Zsg_ds | Ew | Arb | Asl | Asm |
| *Cylindera (Cylindera) germanica* (Linnaeus, 1758) | | | | | | | | 255 | 126 | |
| *Cephalota (Taenidia) elegans* Fischer von Waldheim, 1822 | | | | | | | | | 41 | 3,803 |
| *Cephalota (Taenidia) atrata* Pallas, 1776 | 8 | 4 | | | | 10 | | | | |
| *Cephalota (Taenidia) chiloleuca* Fischer von Waldheim, 1820 | | | | | | | | | 65 | |
| *Calomera littoralis conjunctaepustulata* Dokhtouroff, 1887 | | | | | | | | | | 9 |
| *Cicindela* (s. str.) *campestris* Linnaeus, 1758 | 8 | 6 | 29 | 7 | 13 | | | | | |
| *Carabus (Limnocarabus) clathratus* Linnaeus, 1761 | | | | | | | | 7 | | |
| *Carabus (Tomocarabus) bessarabicus* Fischer von Waldheim, 1823 | 38 | 10 | 10 | 56 | 23 | 6 | | | | |
| *Scarites (Parallelomorphus) terricola* Bonelli, 1813 | | | | | | | | | 43 | |
| *Clivina ypsilon* Dejean, 1829 | | | | | | | | 32 | | |
| *Dyschiriodes* (s.str.) *luticola* (Chaudoir, 1850) | | | | | | | | 63 | 77 | |
| *Broscus cephalotes* Linnaeus, 1758 | | | | | | | | 487 | | |
| *Broscus semistriatus* (Dejean, 1828) | | | | | | | 74 | 506 | 173 | 69 |
| *Tachys* (s. str.) *scutellaris* (Stephens, 1829) | | | | | | | | 25 | 11 | 13 |
| *Bembidion (Emphanes) minimum* (Fabricius, 1792) | | | | | | | | | 27 | |
| *Bembidion (Talanes) aspericolle* (Germar, 1812) | | | | | | | | 87 | | |
| *Cardiaderus chloroticus* (Fischer von Waldheim, 1823) | | | | | | | | | | 71 |
| *Pogonus (Pogonoidius) cumanus* Lutshnik, 1916 | | | | | | | | | | 104 |
| *Pogonus (Pogonoidius) meridionalis* Dejean, 1828 | | | | | | | | | 139 | |
| *Pogonus (Pogonoidius) punctulatus* Dejean, 1828 | | | | | | | | | 18 | |
| *Pogonus* (s. str.) *transfuga* Chaudoir, 1870 | | | | | | | | 540 | 1,676 | 23 |

| HABITATS / SPECIES | Zonal communities | | | | | | Exclave communities | Intrazonal communities | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Zs_ds | Zsg_ds1 | Zsg_ds2 | Za_s | Zgf_s | Zsg_ds | Ew | Arb | Asl | Asm |
| *Pogonistes* (s. str.) *angustus* (Gebler, 1830) | | | | | | | | | | 13 |
| *Pogonistes* (s. str.) *convexicollis* Chaudoir, 1871 | | | | | | | | | | 46 |
| *Pogonistes* (s. str.) *rufoaeneus* (Dejean, 1828) | | | | | | | | | | 96 |
| *Poecilus* (s. str.) *punctulatus* (Schaller, 1783) | | | | 59 | | | | | | |
| *Poecilus* (s. str.) *sericeus* (Fischer von Waldheim, 1823) | 13 | | | 19 | 10 | 14 | | | | |
| *Calathus* (s. str.) *distinguendus* Chaudoir, 1846 | | | | 52 | | | 72 | | | |
| *Calathus* (*Neocalathus*) *ambiguus* (Paykull, 1790) | 38 | 37 | 29 | 3,550 | 190 | 121 | 1,443 | 650 | 1,612 | |
| *Pseudotaphoxenus rufitarsis major* (Fischer von Waldheim, 1823) | 110 | 27 | 145 | 212 | 251 | 161 | | | | |
| *Taphoxenus* (s. str.) *gigas* (Fischer von Waldheim, 1823) | 18 | | 12 | 8 | 7 | 21 | | | | |
| *Amara* (s. str.) *aenea* (De Geer, 1774) | | | | | 60 | | | | | |
| *Amara* (*Xenocelia*) *ambulans* Zimmermann, 1832 | | | 25 | | | | | | | |
| *Amara* (*Amathitis*) *abdominalis* (Motschulsky, 1844) | | | | | | | | | 7 | |
| *Amara* (*Amathitis*) *parvicollis* Gebler, 1833 | | | | | | | | | 5 | |
| *Amara* (*Ammoxena*) *diaphana* Tschitschérine, 1894 | | | 5 | | | | | | | |
| *Curtonotus* (s. str.) *desertus* Krynicki, 1866 | 39 | 6 | 77 | | | 23 | | | | |
| *Curtonotus* (s. str.) *propinquus* (Ménétries, 1832) | | | | | | | | 283 | 169 | |
| *Anisodactylus* (*Hexatrichus*) *poeciloides* Dejean, 1829 | | | | | | | | 22 | | |
| *Dicheirotrichus* (s. str.) *ustulatus* (Dejean, 1829) | | | | | | | | 132 | 282 | |
| *Dicheirotrichus* (*Trichocellus*) *discicollis* (Dejean, 1829) | | | | | | | | 7 | | |
| *Stenolophus* (s. str.) *mixtus* (Herbst, 1784) | | | | | | | | 31 | | |
| *Acupalpus* (s. str.) *elegans* (Dejean, 1829) | | | | | | | | 65 | | |
| *Acupalpus* (s. str.) *parvulus* (Sturm, 1825) | | | | | | | | 38 | | |

| SPECIES / HABITATS | Zonal communities | | | | | | Exclave communities | Intrazonal communities | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Zs_ds | Zsg_ds1 | Zsg_ds2 | Za_s | Zgf_s | Zsg_ds | Ew | Arb | Asl | Asm |
| *Daptus vittatus* Fischer von Waldheim, 1824 | | | | | | | | | 14 | 53 |
| *Harpalus serripes* (Quensel, 1806) | | | 17 | | | 7 | | | | |
| *Harpalus picipennis* Duftschmid, 1812 | | | | | 52 | | | | | |
| *Harpalus anxius* Duftschmid, 1812 | | | | 9 | 40 | | | | | |
| *Harpalus distinguendus* Duftschmid, 1812 | | | | | 32 | | | | | |
| *Harpalus cyclogonus* Chaudoir, 1844 | | 5 | | 16 | 7 | | | | | |
| *Harpalus zabroides* Dejean, 1829 | | | | | 11 | | 40 | | | |
| *Harpalus foveiger* Tschitscherine, 1895 | | | | | 7 | 19 | | | | |
| *Harpalus dispar splendens* Gebler, 1830 | | | | | | | | | 8 | 6 |
| *Ophonus* (*Hesperophonus*) *minimus* Motschulsky, 1845 | 7 | | | | 15 | 11 | | | | |
| *Chlaenius* (*Chlaenites*) *spoliatus* (Rossi, 1790) | | | | | | | | 144 | | 24 |
| *Chlaenius* (*Chlaeniellus*) *tristis* Schaller, 1783 | | | | | | | | 19 | | |
| *Cymindis* (*Tarsostinus*) *lateralis* Fischer von Waldheim, 1821 | 35 | 924 | 32 | 155 | | | | | | |
| *Brachinus* (*Brachinidius*) *costatulus* Quensel, 1806 | | | 13 | | | | | | | |
| *Brachinus* (*Cnecostolus*) *hamatus* Fischer von Waldheim, 1828 | | | | | | | | 94 | 298 | |
| Total species | 10 | 7 | 11 | 11 | 14 | 10 | 4 | 20 | 19 | 13 |
| Total abundance | 314 | 1,013 | 394 | 4,143 | 718 | 393 | 1,629 | 3,487 | 4,791 | 4,330 |

**Note:** Habitats as in Table 1.

reedbeds of an area of 1,000 m² (Fig. 3) more than 13,000 specimens of *H. rufipes* were trapped. Even if we suggest that the entire population of this species from this habitat was exhausted, then during the period of an activity peak (5,500 specimens during the first ten days of July 2006) the population density amounted to about 6 ind./sq. m. This is a very large value. For example, the threshold of injuriousness of *Zabrus tenebrioides*, which is of the same size class as *H. rufipes*, is 2-3 ind./sq. m[*]. Hence, if the captured specimens of *H. rufipes* fed in this habitat and had different contacts with the other species, during this period we would observe changes in demographic parameters of residents. However, this is not the case. The pattern of species accumulation curves, as well as the dynamics of the demographic structure in the populations of resident carabid beetles, did not change over that period (Fig. 10).

Secondly, relatively high numbers and species diversity levels of migrants were recorded at sites which were apparently uninhabited for them. Such an example is a lakeside salt-marsh with high salt concentrations, poor vegetation and soil, as well as occasional floods. In such conditions, only some specialist Carabidae (17 species from the genera
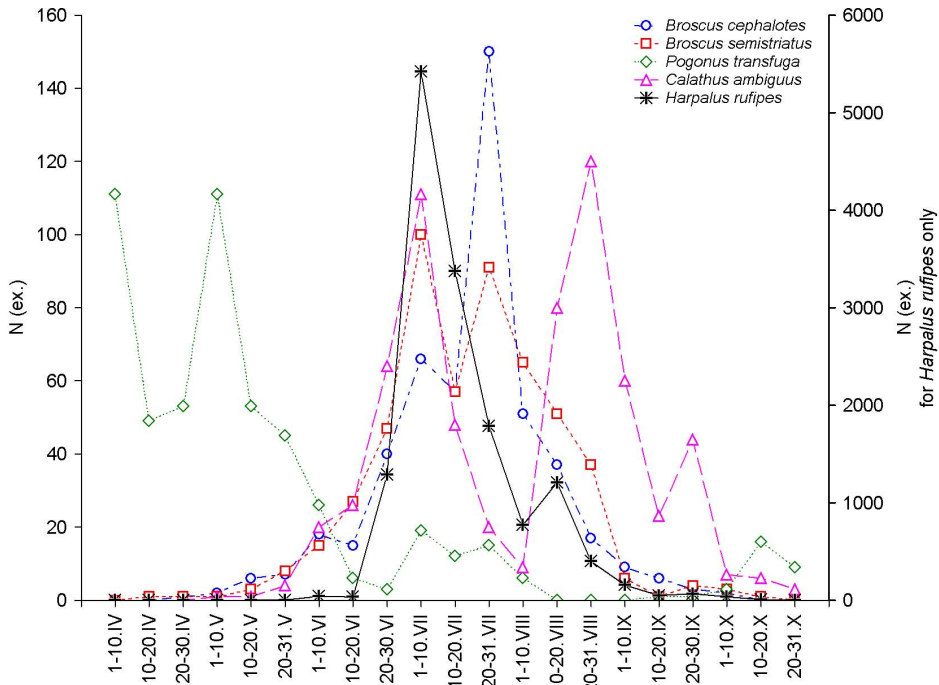


**Fig. 10.** Seasonal variation in abundance curves of *Harpalus rufipes* and four resident carabid species from the reedbed thickets (combined data for 2006/07).

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[*] This estimate is based on the abundance of larvae only (Agrotechnical Bulletin, No4, 2006). A threshold of injuriousness of adults was not determined. However, considering the demographic structure of the population, its value must be lower.

*Cephalotha*, *Calomera*, *Tachys*, *Bembidion*, *Pogonus*, *Pogonistes*, *Cardiaderus*, *Dyschiriodes*, *Poecilus*, *Daptus*, *Dicheirotrichus* and *Harpalus*) can survive. Among 66 species collected in this habitat, 75% cannot live, feed or breed there. Nonetheless, the catching efficiency of several migrants (e.g. the bothrobiont *Pseudotaphoxenus rufitarsis major*) in this habitat was not lower in comparison with that in zonal stations.

Thirdly, our long-term studies show that, in habitable biotopes, some carabid species show all the features of a complete reproduction cycle with clear seasonal peaks even at very low population densities (Fig. 6). Thus, solitary records of species (singletons), of course if the collecting techniques used were adequate, are to be considered neither as an illustration of their rarity nor very low population densities, but as a result of casual migrations.

Unfortunately, we have no direct evidence of interactions between populations of different Carabidae in nature. However, the results of parallel studies on the fauna and demographic structure of individual species show indirectly that the features of structural composition (convergence in size and feeding groups, complementary seasonal activities etc.) are clearly recognized for a small number of residents only in particular habitats. The other carabid species probably form a nearly random complex, which interacts only weakly with resident populations.

Thus, considering the differences in abundance and demographic structure of the populations, we can distinguish three groups in the fauna of Carabidae of the study habitats.

(A) Residents (native species) with their life cycles completely realized in a given habitat. In such species, migrations form only a facultative part of the life cycle. The catches of different species vary widely and sometimes differ by two orders of magnitude.

(B) Migrants are characterized by relatively high numbers, though rarely dominant, but an incomplete demographic structure in particular habitats. Because their reproduction and development are observed in different habitats, their roles in specific assemblages are minor. Migrations form both facultative and obligate parts of their life cycles.

(C) Casual or sporadic species with very low numbers (only with a few records, as a rule), probably associated with a particular habitat during neither migrations nor reproduction.

Both latter groups combined can be termed as "labile components of the fauna", as opposed to "stable components of the fauna" represented by residents. The role of the labile component is still to be proven in the organization of ground beetle communities. Hence, we believe that, from a methodological viewpoint, it is highly important to distinguish between these two components of the fauna in ecological studies of Carabidae.

The ratio of labile to stable components in the study habitats varied strongly and was not always in favour of residents (Table 3). The resident species composed only 6-35% of the species list and 15-90% of the total abundance. In zonal habitats, residents play leading roles and form the main body of the assemblage. More than 65% of the total abundance and 15-35% of the total species diversity make their shares. In azonal habitats, the labile component absolutely prevailed. These species account for about 94% of species composition and about 75% of abundance.

**Table 3.** Species diversity and numerical abundance of stable and labile components of Carabidae complexes in different habitats in the Lake Elton region.

| Habitats | Residents | | Migrants | | Casual species | | Total | |
|---|---|---|---|---|---|---|---|---|
| | Species | Speci-mens | Species | Speci-mens | Species | Speci-mens | Species | Speci-mens |
| Zs_ds | 10 | 314 | 6 | 154 | 12 | 14 | 28 | 482 |
| Zsg_ds1 | 7 | 1,013 | 7 | 86 | 15 | 23 | 29 | 1,122 |
| Zsg_ds2 | 11 | 394 | 9 | 91 | 19 | 31 | 39 | 516 |
| Zgf_s | 14 | 718 | 15 | 113 | 16 | 26 | 45 | 857 |
| Zsg_ds | 10 | 393 | 7 | 26 | 12 | 20 | 29 | 439 |
| Za_s | 11 | 4,143 | 25 | 723 | 28 | 42 | 64 | 4,909 |
| Ew | 4 | 1,629 | 22 | 4,129 | 40 | 64 | 66 | 5,822 |
| Arb | 20 | 3,487 | 36 | 17,893 | 37 | 56 | 93 | 21,429 |
| Asl | 19 | 4,791 | 32 | 4,333 | 26 | 47 | 77 | 9,171 |
| Asm | 13 | 4,330 | 22 | 1,822 | 29 | 43 | 64 | 6,195 |

**Note:** Habitats as in Table 1.

It is important that virtually 2/3 (44 of 71 species) of the migrants fail to breed in any of the study habitats. Thus, the lability of most of the carabid community is not limited by migrations to adjacent habitats, but it seems to be landscape in character (= large scale) and, therefore, must be taken into account in faunistic studies.

The high share of labile components contributes a significant stochastic element to the composition and structure of carabid communities. This makes it difficult to quantitatively evaluate their diversity and faunistic similarity levels. It is noteworthy that the abundance of migrants (estimated through the efficiency of catches) can, and quite often does so by one order of magnitude, exceed that of resident species. Therefore, the statistical consideration of abundant (= dominant) species alone does not solve the problem. Furthermore, in the case of intrazonal habitats, the problem becomes even exacerbated. Thus, the complex of dominants of the reedbeds along the Khara River, as distinguished by the usual criterion (abundance exceeding 5%), discarding the demography of individual species, actually contains only two migrants: *Harpalus rufipes* and *H. distinguendus*. In fact, six resident species form the main body of this community: *Calathus ambiguus*, *Pogonus transfuga*, *Broscus semistriatus*, *B. cephalotes*, *Curtonotus propinguus* and *Cylindera germanica* (Fig. 11).

In this respect, we attempted to evaluate the contribution of the labile component to α- and β-diversity, using measures which have been often applied to faunistic studies (Magurran, 1992). We applied several measures of species diversity and similarity, both for complete and incomplete (including only residents) species lists (Table 4).

The Margalef index showed an expectedly strong dependence on the completeness of species lists, in some cases with 30-fold differences in values noted. On the contrary,
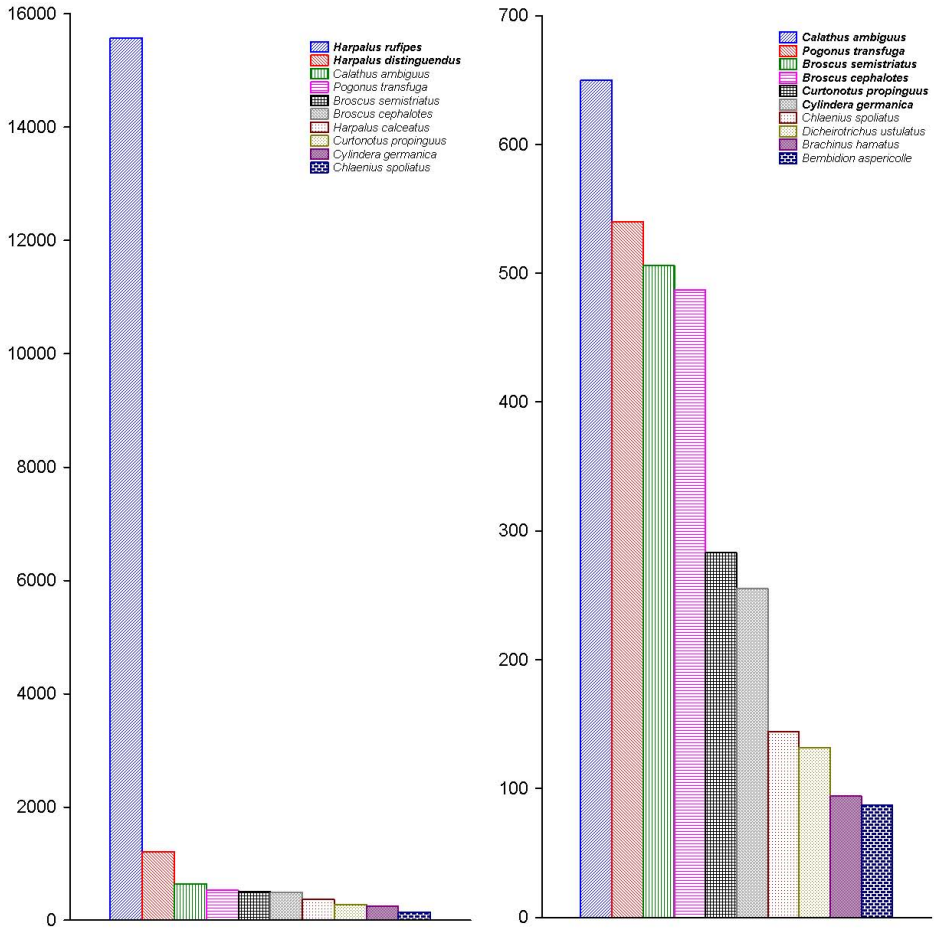
**Fig. 11.** The numbers of ten carabid species most abundant in reedbed thickets with consideration of migrants (on the left-hand side) and only of residents (on the right-hand side). The dominant species are shown by bold-face lines (combined data for 2006/07).

both the Shannon-Wiener diversity index and the Berger-Parker dominance index scaled must better, with the difference in values for complete and incomplete species lists ranging from 2% to 75%. Such degrees of variation could be accounted for by between-habitat differences, causing errors in the measurement of both the species diversity and similarity of separate communities. In most cases both of the latter indices showed lower values for the list of resident species. The only exception was the reedbed carabid community along the Khara River, the bulk of which (9/10) was formed by migrants. In most of the zonal communities, the values of these indices varied the least (below 30% for Shannon-Wiener's diversity index, 25% for the Berger-Parker dominance in-

**Table 4.** Indices of carabid α-diversity in the study habitats of the Lake Elton region.

| Habitats | The Margalef index | | The Shannon-Wiener diversity index | | The Berger-Parker dominance index | |
|---|---|---|---|---|---|---|
| | All species | Residents | All species | Residents | All species | Residents |
| Zs_ds | 4.449 | 1.752 | 2.559 | 2.001 | 0.231 | 0.332 |
| Zsg_ds1 | 3.991 | 1.155 | 0.912 | 0.456 | 0.829 | 0.908 |
| Zsg_ds2 | 5.855 | 0.170 | 2.582 | 1.871 | 0.303 | 0.399 |
| Zgf_s | 5.968 | 2.176 | 0.598 | 0.613 | 0.297 | 0.389 |
| Zsg_ds | 4.636 | 1.687 | 2.113 | 1.658 | 0.357 | 0.400 |
| Za_s | 7.775 | 1.320 | 1.328 | 0.645 | 0.735 | 0.861 |
| Ew | 7.402 | 0.542 | 1.203 | 0.487 | 0.643 | 0.883 |
| Arb | 9.067 | 2.446 | 1.415 | 2.357 | 0.715 | 0.182 |
| Asl | 8.877 | 2.375 | 2.089 | 1.838 | 0.450 | 0.503 |
| Asm | 7.560 | 1.553 | 1.502 | 0.619 | 0.617 | 0.881 |

**Note:** Habitats as in Table 1.

dex), whereas in the intrazonal communities, the variation reached 60-75%. In general, Berger-Parker's dominance index depended less on raw data lists, more clearly selecting the situations with prevailing labile elements. In contrast, the Shannon-Wiener index was more variable and depended more strongly on general diversity.

A comparative analysis of 12 dendrograms created using two indices of similarity and three clustering algorithms, showed a rather complex pattern (Fig. 12). As one would expect, the cluster of zonal habitats with low diversity and abundance levels of resident species (*Zs_ds*, *Zgf_s*, *Zsg_ds2*, *Zsg_ds* and, usually, *Zsg_ds1*) was very stable regardless of the way of calculation and of the count of labile elements. The results concerning the other habitats varied more strongly depending both on the index used and the set of input data (e.g. consideration of migrants). In this respect, two things seem to be of special interest.

Firstly, the differences in estimating the salt-marsh lakeside fauna (*Asm*) are noteworthy. If we analyzed the complete species list of Carabidae trapped there, then this peculiar habitat always grouped together with the azonal and most of the mesophytic zonal habitats. Its position changed appreciably, sometimes unexpectedly, from one similarity measure and one way of clustering to another. Calculations based on an incomplete species list (for residents only) showed an adequate degree of isolation of this carabid community with all of the clustering methods applied.

Secondly, the use of the complete species list in combination with different methods of calculation led to significant variation in the classification of communities with large proportions of migrants. Thus, the position of the reedbed carabid community (*Arb*) varied strongly. In different cases it grouped together with intrazonal (*Asl*), zonal (*Za_s*) or exclave (*Ew*) habitats. In contrast, an analysis of the residents showed a similar pattern of clustering regardless of the method of similarity evaluation.
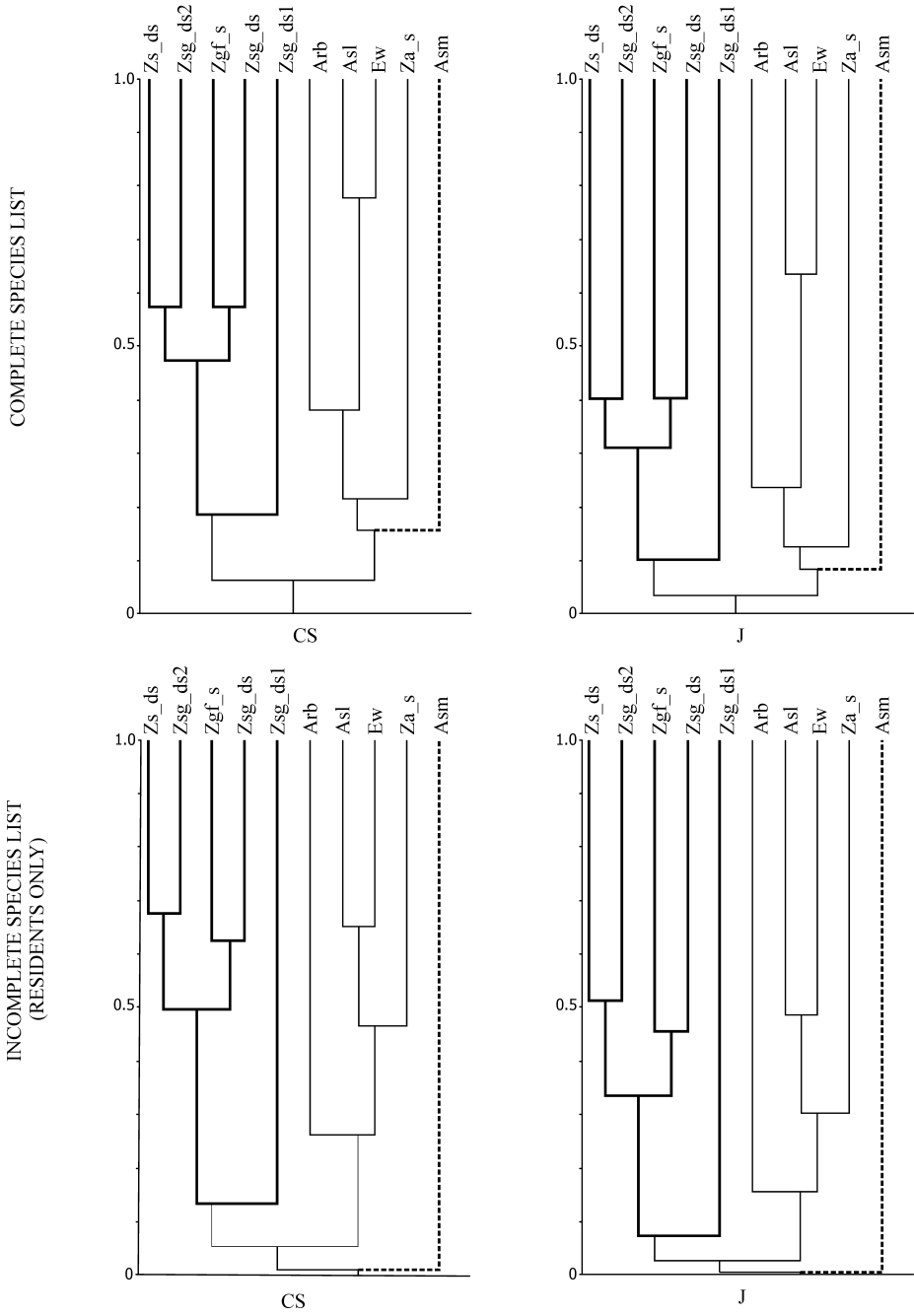
**Fig. 12.** Dendrograms of habitat similarity using the Czekanowsky-Sørensen index (left column) and Jaccard's coefficient (right column), both clustered by the unweighted mean method. The constant complex of zonal habitats is shown by bold-face lines, the salt-marsh lakeside by a dotted line.

## CONCLUSION

Thus, our knowledge of the local faunas of Carabidae, as well as the methods of their study requires serious corrections to be made. The species diversity both of separate habitats and landscapes in general is to ⅔-s extent composed of non-resident species. The species lists compiled on the basis of standard trapping surveys appear to satisfactorily show the real composition of zonal habitat assemblages only. In general, the species compositions which are highly variable in space and time substantially reduce the avail- ability of faunistic checklists based on standard collecting methods for geozoological and zoogeographical analyses.

In this respect, the distinction between the terms "local fauna" and "concrete fauna" seems to be reasonable (Penev, 1997). Similar to floristics (see Shelyag-Sosonko, 1980), the elementary unit of a faunistic analysis suitable for zoogeographical reconstructions is to be termed a concrete fauna, i.e. one which is characterized by its own territorial and structural continuity, history etc. An acceptable determination of the concrete fauna closely depends on the correct distinction of stable and labile components.

The results of our study, as well as a critical analysis of pertinent literature sources, allow us to outline at least two possible ways for improving the reliability of faunistic species lists.

(1) The first step is to reduce the study period to one season, but with an increased intensity and variety of collection methods employed. The trivial and migratory species are represented in faunistic lists much better under long-term observa- tions, because their availability is largely determined by environmental condi- tions. As shown above, collection with the use of a variety of techniques during one season allowed the completion of equally comprehensive species lists, and thereby ones which were strongly related to the current climatic situation.

(2) The second step is reducing the scope of the model group to be used. The choice of taxa with more or less uniform migratory capacities and other ecological parameters as an object of faunistic studies increases their applicability to zoogeographical analyses. Moreover, relatively short-term, rapid assessment methods can be used. In this respect, the analysis of the local faunas of European *Carabus* (Penev & Turin, 1994; Penev, 1996; Penev et at., 2003) appears to be correct while that of the local faunas of all Carabidae of the Ural Mountains (Kozyrev et al., 2000) does not.

The ratio of stable to labile components in individual assemblages of Carabidae must be expected to change considerably between different natural zones. Therefore, it would seem desirable to conduct a series of similar studies by independent groups of carabidologists in order to compare the efficiency of standard collecting techniques in different landscapes and habitats.

## ACKNOWLEDGEMENTS

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