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Long-term dynamics and spatial distribution of stable and labile components in ground beetle communities (Coleoptera: Carabidae) in a mosaic of flood-plain meadows

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Abstract

Background and purpose: *Long-term changes in the community structure of ground beetles were surveyed in nine flood-plain meadows of the Oka River valley (Ryazan Region, Russia) using the concept of stable-labile components. Such approach contradicts with the traditional estimation of the community structure, and there are only a few similar studies now.*

Material and methods: *Based on inundation time, all model habitats were divided into three groups: dry, short-term flooded, and long time flooded meadows. Beetles were trapped from mid-April to late September 2006 and from early April to late October in 2007 and 2008 using pitfall traps. All captured beetles were dissected and the conditions of their gonads were evaluated.*

Results and conclusions: *Altogether, 142 species from 50 genera were recorded. In terms of abundance, 84% of all specimens belonged to 22 species (15.5% of the total species diversity). However, neither in all years nor in all study habitats the local populations of dominant species are characterized by a complete demographic structure. On the contrary, 49 species were residents, but only from three to 27 of them completed their life cycles at least in one habitat. In total, the labile component usually had a higher species diversity, but the stable component was more abundant. Large-scale migrations were typical solely of stenotopic species that inhabit only few meadow types. Eurytopic species were easy to redistribute in a limited area and occupied all available habitats. In some species, not only migrations, but also changes in life cycles from annual to biennial ensured the survival of their local populations.*

INTRODUCTION

Flood-plain meadows are among the best-known unstable and variable ecosystems. The environmental conditions in these habitats vary annually under changing weather parameters and hydrological regimes *(1)*, and significantly affect the abundance and distribution of terrestrial arthropods *(2, 3)*.

It is noteworthy that annual fluctuations of the environmental conditions in flood-plain meadows can render a strong impact on the dynamics and activity of certain ground beetle species (Coleoptera: Carabidae), their spatio-temporal distribution, as well as on the structure of the community as a whole *(4, 5, 6, 7, 8, 9, 10)*.

Figure 1. *Study area (habitats as in Table 2).*

This paper deals with the community structure of Carabidae in different types of flood-plain meadow using the concept of stable-labile components *(11)*. The main point of this concept is that the regular change in the physiological condition that allows for a reconstruction of the life cycle at the local population scale, but not the abundance of the species, must be regarded as the criterion for the successful existence and breeding of a population in a particular habitat. Such approach really contradicts with the traditional estimation of the community structure of ground beetles. Unfortunately, there are only a few studies on the structure of Carabidae communities which applies the concept of stable-labile components *(12, 13, 14)*. However, we hope that the current paper will be stimulated similar studies in nearest future.

MATERIAL AND METHODS

Study area

Ground beetle communities of nine meadows in the flood-plain of Oka River within the Oka Biosphere Nature Reserve (Ryazan Area, Russia – 54°43'58"N 40°58'42"E) were studied (Fig. 1). Based on inundation time, all model habitats were divided into three groups: high-level meadows (I) never flooded during our study; intermediate meadows (II) characterized by short-term inundations, and low-lying meadows (III) which were flooded for long time periods each year (Fig. 2).

Weather conditions and the inundation regime per habitat in different years of this study are presented in Table 1. Long-term average data on the weather and hy-

Table 1. *The weather and hydrological conditions in the middle course of Oka River*

Weather and hydrological phenomena	2006	2007	2008	Long-term average data
Date of snowmelt	17th April	21st March	29th March	8th April[1]
Sum average temperature from April to October, °C	2763.4	3015.9	2903.7	2653.6[1]
Average monthly temperatures from April to October, °C	12.9	14.1	13.5	12.4[1]
Sum rainfall from April to October, mm	564.0	335.8	465.3	403.7[1]
The maximal level of flood in the Oka River, cm	570	519	479	557[2]
Total duration of flood in the Oka River, days	39	23	17	33[2]
The maximal level of flood in the Pra River, cm	342	329	324	332[3]
Total duration of flood in the Pra River, days	57	29	47	38[3]

Notes: 1 – 1938-2010 *(15, 17)*, 2 – 1935-2010 *(16, 18)*, 3 –1952-2010 *(16, 18)*.

Figure 2. *Model habitats: 1 – dry forb-grass meadow, 2 – forb-grass meadow with* Carex leporina, *8 – grass-forb meadow, 7 – herb meadow with* Alopecurus pratense, *4 – wet meadow with* Galium boreale *and* Bromopsis inermis, *5 – sedge-rich meadow with* Lythrum virgatum *and* Digraphis arundinacea, *6 – wet sedge-rich meadow, 9 – wet meadow with legumes and sedges, 3 – sedge-rich bog meadow (photos by Olga Trushitsyna, 1, 8, 7 – in June 2006; 2-3, 4-6, 9 – in July 2008).*

Table 2. *Characteristics of the model habitats*

Group of habitats	Habitats	Date of the end of inundation and the setting of traps			Soil moisture (average for season, according to Ramensky, 1938)			Maximum projective cover, % (according to Braun-Blanquet, 1964)		
		2006	2007	2008	2006	2007	2008	2006	2007	2008
I	1	22.04	02.04	01.04	2.0	1.5	1.5	40	25	60
	2	22.04	02.04	01.04	2.5	1.5	2.0	70	30	80
	8	22.04	02.04	01.04	2.5	1.5	2.0	80	45	90
II	7	02.05	12.04	01.04	2.5	2.0	2.0	95	100	100
	4	12.05	12.04	01.04	3.0	2.5	3.0	100	85	100
III	5	22.05	12.04	11.04	3.5	2.5	3.5	100	90	100
	6	01.06	22.04	01.05	4.0	2.5	4.0	100	90	95
	9	22.05	22.04	11.04	4.5	2.5	4.0	95	90	95
	3	21.06	12.04	01.04	5.0	3.5	4.5	100	85	100

Notes: 1 – dry forb-grass meadow, 2 – forb-grass meadow with *Carex leporina*, 8 – grass-forb meadow, 7 – herb meadow with *Alopecurus pratense*, 4 – wet meadow with *Galium boreale* and *Bromopsis inermis*, 5 – sedge-rich meadow with *Lythrum virgatum* and *Digraphis arundinacea*, 6 – wet sedge-rich meadow, 9 – wet meadow with legumes and sedges, 3 – sedge-rich bog meadow. The meadows are ranked according to soil moisture.

drological conditions follows Onufrenya *(15, 16, 17, 18)*. According to these data, the cool and wet conditions of 2006, with a high and prolonged inundation, was the most typical year as regards the weather and hydrological conditions for the study area, while 2007 and, especially, 2008 were the most atypical, being dry and hot and characterized by low levels and the shortest duration of inundations in the Oka River valley. The temperature in 2008 was more similar to the long-term observation data, but the rainfall sum was considerably higher.

Collecting methods

Beetles were trapped using plastic pitfall traps of 0.5 l capacity (Ø 95 mm) with 4% formalin as a fixative. In each habitat, ten traps were arranged along a transect at 10 m intervals. The traps were set as follows: three at high-level, two at intermediate-level, and four in low-level meadows. The traps were checked every ten days, and all captured beetles were dissected for inspection of gonads.

Time of survey

The traps were set from mid-April to late September 2006 and from early April to late October in 2007 and 2008. The timing of the first sampling was determined by the time of water release and the end of an inundation (Table 2).

Terminology

Soil moisture was evaluated according to Ramensky's ranks *(19)*, while the projective cover as the relative projected area of the vegetation on the soil surface was estimated following Braun-Blanquet *(20)*.

Based on gonad conditions *(21, 22, 23)* and the degree of wear-and-tear of the mandibles *(24, 25)*, six physiological states in the adults of both sexes (teneral, immature, mature of parental and ancestral generations, as well as the spent of parental and ancestral generations) were determined *(12)*.

Species with an abundance rate exceeding 5% were regarded as dominants *(26)*. On the other hand, according to the demographic structure of the local populations three groups of the species were considered as well: residents, migrants and sporadic. In residents, the demographic structure of the local populations is complete, and their habitats are the residential. In migrants and sporadic species, the demographic structure of the local populations is incomplete, and their habitats are the transit. Migrants and sporadic species represent a labile component in ground beetle communities, as opposed to a stable component, represented by residents *(11, 12)*.

The typology of the life cycles follows Matalin *(27)*, while that of the communities of soil arthropods follows Kuznetsova *(28)*.

The taxonomy of Carabidae follows the catalogue of Palaearctic Coleoptera *(29)*.

Statistics

Statistical analyses were performed using STATISTICA 8.0 *(30)* and PAST 3.10 software *(31)*. The similarities between the assemblages of ground beetles in different types of meadows were calculated using Jaccard's coefficient of community, as well as the Bray-Curtis dissimilarity index. These were followed by clustering using unweighted pair groups with the arithmetic means (UPGMA) method *(32)*.

Table 3. *Abundance (%) of the dominant species of ground beetles in flood-plain meadows of the Oka River valley.*

No	Species	Years	Habitats									HD
			I			II		III				
			1	2	8	7	4	5	6	9	3	
1.	*Carabus granulatus*	2006	0.3	**6.2**	**10.7**	**9.3**	**14.2**	**13.7**	**12.8**	**16.9**	**5.8**	8
		2007	0.2	4.6	3.3	4.6	**6.3**	**9.1**	**9.2**	**16.6**	**9.4**	5
		2008	0.2	1.3	1.9	1.8	3.5	**10.9**	4.0	**13.9**	**13.9**	4
2.	*Clivina fossor*	2006				0.1	1.7	4.2	**5.4**	2.9	0.3	1
		2007				0.1	0.6	2.9	3.8	2.5	0.4	
		2008					0.1	1.3	2.8	2.9	0.2	
3.	*Trechus secalis*	2006		2.3	0.1	0.2	0.1		0.2		0.1	
		2007	0.2	0.7	0.6	0.3	0.5	0.5	0.4	0.1	**6.6**	1
		2008	0.2	0.3	0.9	0.1	0.3	0.4	0.3	0.2	4.9	
4.	*Bembidion gilvipes*	2006		2.6	0.1	0.3	**5.9**	**6.0**	**6.0**	1.6	**5.1**	4
		2007		**5.9**	0.1	0.3	**6.3**	**15.0**	**5.6**	**5.2**	**10.0**	6
		2008		0.4	0.1	0.2	4.9	**6.1**	**5.8**	4.8	**7.9**	3
5.	*Poecilus versicolor*	2006	**33.6**	**33.5**	**38.2**	**20.0**	**22.2**	2.7	**5.1**	0.7	0.2	6
		2007	**6.4**	**22.9**	**24.6**	**19.8**	**24.2**	**19.9**	**25.5**	**18.2**	**7.3**	9
		2008	**5.9**	**52.4**	**9.6**	**31.4**	**22.8**	**21.7**	**25.2**	**14.1**	**5.9**	9
6.	*P. lepidus*	2006	**7.0**	4.6	2.0	0.4						1
		2007	**6.0**	3.3	3.5	0.7						1
		2008	**7.2**	**6.2**	**8.9**	0.7	0.1					3
7.	*Pterostichus vernalis*	2006	0.2	0.5	0.0	0.1	0.4	0.4	2.0	0.4		
		2007	0.2	0.5	0.2	0.3	0.3	0.1	1.8	1.0	1.2	
		2008	0.0	0.4	0.0	0.6	0.3	0.6	**5.1**	1.2	1.4	1
8.	*P. anthracinus*	2006	0.7	1.0	0.3	1.4	3.3	**14.4**	**16.6**	**10.6**	**14.9**	4
		2007	1.0	1.4	1.0	2.4	0.9	2.3	1.3	4.0	4.3	
		2008	1.0	0.7	0.5	1.3	0.6	4.3	**6.8**	**5.6**	3.9	2
9.	*P. nigrita*	2006		0.8		0.2	1.0	1.5	2.4	2.3	**6.9**	1
		2007	0.4	1.2	0.2	0.3	0.2	0.6	1.2	0.7	2.3	
		2008	0.2	0.1	0.2	0.2	0.2	0.4	2.2	0.8	3.8	
10.	*P. melanarius*	2006	0.2	1.0	1.9	**12.0**	**9.0**	**17.7**	**5.2**	**5.7**	**6.2**	5
		2007		0.2	1.4	**32.7**	**23.6**	**17.9**	**18.2**	**28.6**	**16.1**	5
		2008		0.4	0.4	**17.6**	**34.9**	**27.0**	**15.7**	**22.0**	**8.4**	5
11.	*Calathus fuscipes*	2006	2.4	0.3	0.1	0.1						
		2007	**15.6**	0.2	0.3	0.1						1
		2008	**18.8**	0.3	2.7							1
12.	*C. melanocephalus*	2006	1.6	3.3	2.0	0.9	0.4		0.1			
		2007	**5.6**	4.7	1.9	1.6	1.5	0.6	1.6	0.2	0.6	1
		2008	0.8	2.7	**5.4**	**6.0**	0.3		2.0	0.1		2
13.	*Agonum viduum*	2006		0.9	0.0	0.2	0.7	1.6	**8.0**	**23.1**	**10.0**	3
		2007		0.3	0.1	0.1		0.1	0.6	0.9	0.5	
		2008		0.4	0.1	0.1	0.1	1.2	1.8	4.8	1.4	
14.	*A. fuliginosum*	2006		2.3	0.1	0.4	0.1	0.1	0.6	0.4	2.1	
		2007		**6.4**	0.1	0.5		0.1	0.3	0.6	1.3	1
		2008		2.0	0.1	0.3		0.1	0.2	0.2	1.3	
15.	*Amara equestris*	2006	2.1	1.7	1.3	0.4	0.1					
		2007	**15.8**	**9.6**	**6.9**	2.1						3
		2008	**8.8**	2.4	**11.4**	1.6						2
16.	*Harpalus rufipes*	2006	**14.6**	**7.1**	**19.3**	**27.0**	**10.5**	**17.5**	1.6	0.8	0.7	6
		2007	**14.0**	**16.6**	**19.4**	**11.8**	**8.1**	2.8	0.8	0.5	0.5	5
		2008	**20.1**	**11.2**	**20.6**	**12.7**	**7.2**	1.5	0.2	0.4	0.3	5
17.	*H. rubripes*	2006	**5.7**	**5.2**	0.4		0.1					2
		2007	**5.6**	2.1	1.3	0.2	0.1				0.1	1
		2008	4.6	3.3	0.7				0.1		0.1	

		2006	0.8	1.8	1.6	**6.4**	**6.6**	3.5	2.4	1.0	0.7	*2*
18.	*H. latus*	2007	1.6	0.5	1.2	3.6	**5.5**	**7.8**	4.5	1.8	1.4	*2*
		2008	1.8	0.3	**8.7**	**5.0**	4.7	3.4	1.8	3.3	0.3	*2*
		2006	1.6	0.2	**5.2**	3.5	0.3	0.1	0.1			*1*
19.	*H. luteicornis*	2007	2.4	0.3	**17.7**	2.0	1.7	0.2	0.2			*1*
		2008	2.6	0.6	**16.6**	3.0	0.8		0.1			*1*
		2006	**7.8**	0.1								*1*
20.	*H. smaragdinus*	2007	2.4		0.1	0.1						
		2008	**9.1**	0.1	0.1							*1*
		2006	**5.8**		1.4	0.2						*1*
21.	*H. affinis*	2007	2.4		0.8	0.1						
		2008	2.7	0.1	1.2							
		2006		**8.5**	0.2	3.9	**7.6**	**7.8**	**13.6**	**22.8**	**21.6**	*6*
22.	*Oodes helopioides*	2007	0.2	3.1	0.5	2.4	4.1	3.6	4.2	**8.3**	**12.3**	*2*
		2008		**7.8**	0.2	1.8	1.8	**5.8**	**10.5**	**9.0**	**22.9**	*5*
Total dominant species		2006	6	6	4	5	7	6	8	5	6	
		2007	7	5	4	3	6	5	4	5	7	
		2008	6	4	7	5	3	5	6	5	5	

Notes: **bold** – dominant species, *HD* – number of habitats where each species dominated, habitats as in Table 2, groups of habitats as in the above text.

RESULTS

Species diversity and dominant structure

During the entire period of observation, more than 52,700 specimens of Carabidae belonging to 142 species were collected. Six genera were characterized by high levels of species diversity, as follows: *Amara* – 17 species, *Harpalus* – 13 species, *Pterostichus* – 12 species, *Bembidion* – 11 species, *Agonum* – ten species, and *Carabus* – seven species (Appendix).

The highest species diversity of the genera *Amara* and *Harpalus* was observed in the flood-free and short-term inundated meadows, while species of the genus *Ophonus* were recorded only in the flood free habitat. Mesophilic and meso-xerophilic species of these genera were most diverse and abundant there. Hygrophilous and meso-hygrophilous species of the genera *Pterostichus*, *Bembidion*, *Agonum* and *Carabus* were observed in almost all habitats, but they were abundant only in short- and/or long-term inundated meadows. Species of the genera *Agonum* were more diverse in long-term inundated meadows.

In dry and short-term inundated meadows 63-89 species were recorded, while 61-67 species were occurred in long-term inundation meadows (Appendix). During different years, 36-69 species were found in each of the study meadows, but only three to eight species prevailed, as a rule. The complex of dominant species included 22 species, comprising 15.5% of the species diversity and 84% of the total abundance. However, in different years, the composition of dominant species in the same habitat varied strongly. Eight species, *Carabus granulatus, Bembidion gilvipes*, *Poecilus versicolor, P. lepidus*, *Pterostichus melanarius, Harpalus rufipes, H. latus* and *Oodes helopioides*, were dominants over all three years of our study, while other species (*Agonum viduum*, *Pterostichus nigrita*, *Amara equestris, Calathus fuscipes*, *Harpalus luteicornis* etc.) prevailed only in certain years (Table 3).

Some species, such as *P. versicolor*, *C. granulatus*, *P. melanarius* and *H. rufipes*, prevailed in most types of meadows. At the same time, *P. melanarius* was virtually absent from dry meadows, while *H. rufipes* showed a very low abundance in long-term flooded lowland habitats, and only *P. versicolor* dominated in all types of meadow, except in 2006. The meso-xerophilic *Harpalus smaragdinus*, *H. rubripes*, *H. luteicornis* and *P. lepidus*, as well as the xerophilic *A. equestris* and *C. fuscipes*, were more abundant in permanently dry meadows. However, *H. luteicornis* was affiliated with the dominants only in a grass-forb meadow, while *C. fuscipes* and *H. smaragdinus* were recorded as dominants only in a dry forb-grass one. In wet lowland habitats, the hygrophilous *B. gilvipes, P. nigrita, P. vernalis, P. anthracinus, A. viduum*, *A. fuliginosum* and *O. helopioides* were characterized by higher abundance levels, but *P. nigrita* was more abundant only in a sedge-rich bog meadow.

Stable-labile components structure

At the same time, 49 species (35% of the total species list) were considered as residents, 57 species (40%) were recorded only as sporadic, while 36 species (25%) were recognized either as sporadic or migrants. All mentioned above 22 dominant species belonged to the assemblage of resident species. It is noteworthy that from three to 27 residents were capable of completing their life cycles at least during one year and at least in one habitat. Among these, only *P. versicolor* was able to reproduce in all habitats during all three years of the study. Two species, *C.*

granulatus and *P. melanarius*, completed their life cycles in seven and six habitats, respectively, during the study period. The range of annual variation in the number of residential habitats for individual species owing to changes in air temperature and inundation reached 1.5-3 times (Appendix).

During the three years of the study, in almost all habitats the labile component (migrants and sporadic species) had the highest species diversity, which, however, decreased gradually from permanently dry meadows to long-term inundated ones. The species diversity of the residents increased distinctly, but on average did not exceed 40% in this series. At the same time, in all meadows during all years, the stable component prevailed and the abundance of residents on average did not fall below 50%. However, permanently dry meadows were characterized by the highest abundance of the labile component. In certain habitats during different years, the proportion of migrants in the total abundance varied widely from 14.5% to 56.8% (Fig. 3).

The dominance structure differed considerably between the full and limited (residents only) species lists for those habitats. For example, in 2007 the community of ground beetles of the dry forb-grass meadow could be recognized as polydominant, in which the abundance of seven species exceeded 5%. However, among 45 species collected in this habitat, only three were recognized as residents. Thus, this community had to be characterized as oligodominant (Fig. 4A). A similar pattern was observed in our analysis of the carabid community structure of the forb-grass meadows with *Carex leporina*. In most other study habitats, the structure of Carabidae communities was characterized as polydominat, as distinguished both by the usual criterion of dominance and by the criterion of stable-labile components. Nevertheless, among the dominant species in the ground beetle communities of some permanently dry meadows, as well as some short-term inundated meadows, one or two migrant species were recorded as well. The aspect of the communities of ground beetles in all long-term inundated meadows, regardless of the approach used, was virtually identical (Fig. 4B).

Community ordination

A comparative analysis of the results of clustering the carabid communities with consideration of the labile component (complete species lists) and only of residents showed different patterns in several cases.

When using the complete species list for the ordination of communities based on Jaccard's coefficient, habitat vicinity was established first of all. In this case, the adjacent meadows grouped together, as a rule, while the dry forb-grass meadow was not only segregated from all riparian meadows inundated permanently, but also from other dry and short-term inundated habitats (Figs 1, 5A). In contrast, the use of the residents' lists alone (stable component) ensured the grouping of habitats according to their microclimatic conditions, especially the soil moisture and the projective cover (Table 2). The clusters of dry and short-term inundated meadows, on the one hand, and long-term inundated meadows, on the other hand, were clearly separated from each other. At the same time, not the adjacent habitats, but the habitats with similar humidification modes showed the greatest faunal similarity to each other (Figs 1, 5B). Thus, in this case the ordination of communities according to the list of residents alone appeared to be more adequate than that which considered full species lists.

The ordination of the communities of Carabidae based on Bray-Curtis index both for the abundance of all recorded species or resident species only produced the same result. The high abundance of residents in all study habitats, as well as the similar environmental conditions during certain years were the main determinants of Carabidae community similarity of the study habitats.

Long-term dynamics and spatial distribution of stable-labile components

The proportions of the stable and labile components in all of the habitats studied varied widely over the three years of observation. In 2007, in the ground beetle communities of all non-flooded meadows, as well as of one short-term inundated meadow, the proportion of resident species and their abundance sharply decreased by 14.8-30.5%. In the communities of carabids of most of the long-term inundated meadows, however, the share of the stable component, as well as its abundance, were virtually invariable and increased only a little (< 10%). During 2008, the proportion of resident species, as well as their abundance in dry meadows, reached or, in some habitats, even exceeded the 2006 level. In the long-term inundated meadows, the relative species diversity and abundance of resident species remained unchanged or decreased insignificantly (Appendix).

The annual variations in the abundance of meso-xerophilous species did not exceed 3-3.5 times. These species showed the greatest fidelity to the habitats they occupied and occurred mainly in permanently dry (*C. fuscipes*, *A. equestris*) or short-term inundated meadows (*H. luteicornis*). However, even in the favourable, dry and hot years 2007 and 2008, none of these species used wet inundated meadows as a residential habitat; nor did they utilize such places even as transit habitats, despite quite similar soil moisture levels, they shared (Table 2).

Substantial annual fluctuations in abundance, both in residential and transit habitats, were typical of hygrophilous species inhabiting wet long-term inundated meadows. During the coolest and wet season of 2006, the abundance of *P. anthracinus* and *A. viduum* in residential habitats exceeded their abundance in the transit habitats

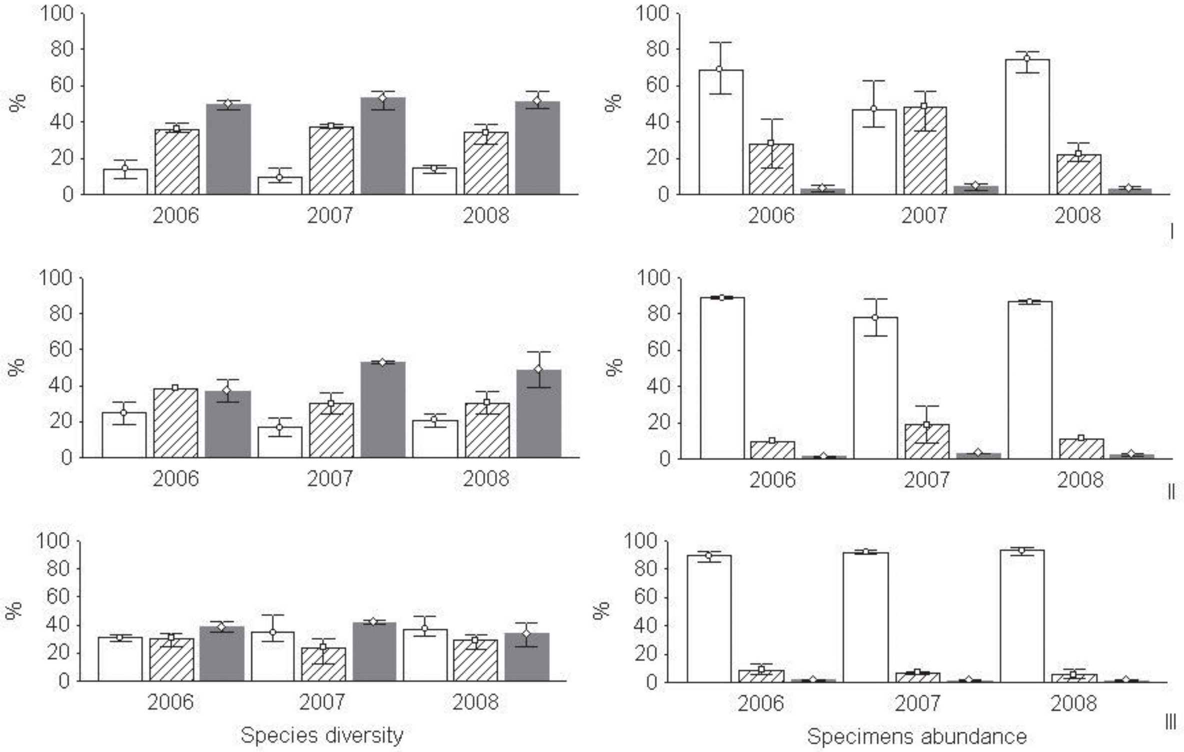

Figure 3. *Variations in the proportion of stable and labile components in different groups of flood-plain meadows of the Oka River (white bars – residents, hatched bars – migrants, gray bars – sporadic species, whiskers – SD, groups of habitats as in the above text).*

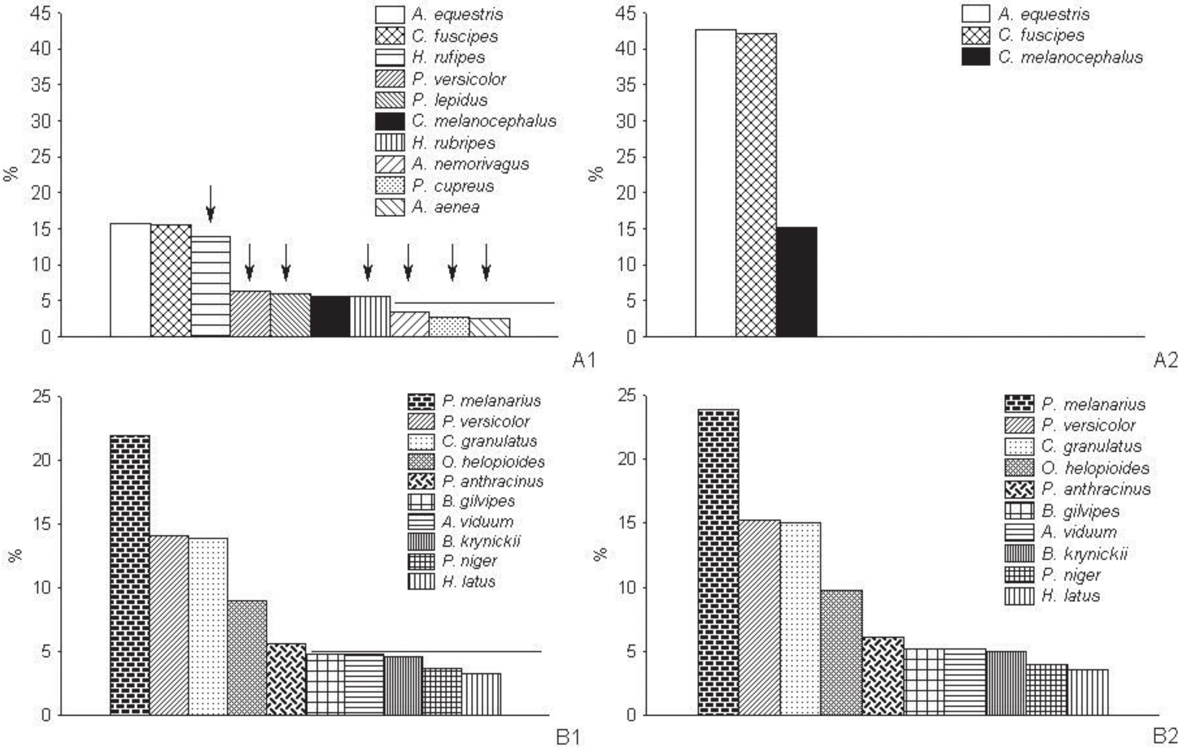

Figure 4. *Structure of Carabidae communities of dry forb-grass meadow (A), of wet meadow with legumes and sedges (B), based on the numbers ratio of ten most abundant species (A1 and B1), and the resident species (A2 and B2), A – data for 2007, B – data for 2008 (line delimiting the level of dominants, arrows indicate the migrants).*

more than 16 and 22 times, respectively. However, in the hot and dry 2007, the numbers of each of those species in residential habitats were only 1.5 times higher than in transit ones. During the more favorable 2008, the abundance of both species in residential habitats again exceeded that in transit habitats. At the same time, the total abundance of *P. anthracinus* in 2008 barely exceeded half of the total numbers in 2006, while the abundance of *A. viduum* in 2008 was almost 3.5 times lower than in 2006.

The abundance of eurytopic spring breeders such as *C. granulatus*, *P. versicolor* and *H. latus* remained virtually unchanged over all three years. The high mosaic of soil and vegetation conditions within a relatively small area, as well as their ecological flexibility, allows these species to selectively occupy the most suitable habitats. In the wet year they used some permanently dry meadows as residential habitats, while in the dry years they moved into temporarily flooded lowland places. Due to this reallocation, the abundance of these species in the residential habitats maintained at a high level throughout the three years of research (Appendix).

Last but not least, the abundance of the autumn breeders *P. melanarius* and *H. rufipes* during the three years was remained very high, although it varied considerably under the influence of environmental conditions. *Pterostichus melanarius* did not use permanently dry meadows for breeding, while even in hot and dry years, *H. rufipes* failed to colonize inundated lowland habitats (Appendix).

DISCUSSION

The ground beetle fauna of the meadows of the Oka River valley is typical of the flood-plain grasslands of the Central Russian Upland. Most of the species are also known from the neighboring regions e.g. 131 species form the grasslands of the Moscow Area *(33, 34)*, 123 species from the greenlands of the Lipetsk Area *(35)*, 95 species in the meadows of the Bryansk Area *(36)*, 86 species in the grassland of Belarus *(37, 38)*, and 75 species in dry and wet meadows of Mordovia *(39, 40)*.

Nevertheless, the species diversity of ground beetles both of the flood-plain as a whole (142 species) and in particular habitats (36-69 species) was higher as compared to other regions of the European part of Russia and of other countries of Europe, e.g.: in the Bryansk Area, 22-56 species have been recorded from wet flood-plain meadows, 18-66 species in dry meadows *(41)*; 56 species in the flood-lands of the Nizhny Novgorod Area, *(42)*; 14-45 species in wet meadows of Mordovia *(39, 40, 43)*, 54-57 species in the flood-plain meadows of the Berezinsky Nature Reserve, Belarus *(37, 38)*, from 39 to 45 species in the flood-plain meadows of the Vyatka River, Nurgush Nature Reserve, Russia *(44)*; in the meadows of northern boreal forest in the Arkhangelsk Area, Russia 91 species in various habitats *(45, 46, 47)*. In Central and Western Europe, different types of meadow support up to 52 carabid species, as a rule *(48, 49, 50, 51)*. For example, from 7 to 24 species of carabids were recorded during three years in different grasslands of the Limburg Nature Reserve, Germany *(7)*, versus 13 to 43 species in the meadows of the Mazovian Lowland, Poland *(6)*.The high species diversity of Carabidae in the study flood-plain meadows can be accounted for by relief heterogeneity and highly mosaic distributions of plant associations. As flat patches alternate with local elevations and wetlands depressions, species with diverse ecological preferences can find suitable habitats. The vicinity of habitats with different soil and vegetation conditions ensure migrations and species turnover; this also increases the species diversity of ground beetles both in general and per particular habitat. In addition, long-term observations and the conservation of undisturbed habitats in the nature reserve also helps in maintaining the high species diversity of ground beetle communities of flood-plain meadows.

At the same time, the composition of dominants in the Carabidae communities of flood-plain meadows of the Oka River fails to differ strongly from similar compositions formed in the meadows within the entire forest zone. As a rule, *P. versicolor* and *P. melanarius* are the most abundant species that prevailed virtually in all types of meadow in Europe *(6, 39, 41, 42, 43, 45, 46, 51, 52, 53)*.

However, neither in all years nor in all study habitats dominant species are characterized by a complete demographic structure. In such cases, despite their high abundance, these species are only to be considered as migrants, while the places they occur in should be regarded as transit habitats *(11)*. Apparently, the community structure drawing a clear difference between the migrants and non-migrants would differ significantly (Fig. 4A).

From 61 to 89 species were recorded in the studied meadows, but only three to 27 species completed their life cycles during certain years in particular habitats (Appendix). These results correspond well with those of previous studies. In the agricultural landscapes of the Kuban-Azov Lowland, most fields and forest shelter belts were shown to be transit habitats for many carabid species *(54)*. According to the results of our studies, the abundance of the labile component (migrants and sporadic species) in some habitats can be much higher, often even exceeding, the numbers of the stable component, *i.e.* resident species *(9, 11, 12)*.

It is noteworthy that, in different climatic zones, the proportions of the stable and labile components change in a series of similar habitats. In open flood-plain habitats of the forest zone, the species diversity and abundance of the stable component correlate positively with an increase in soil moisture and projective plant cover. At the same time, the labile component is most diverse in permanently dry meadows, while its abundance averages one-third

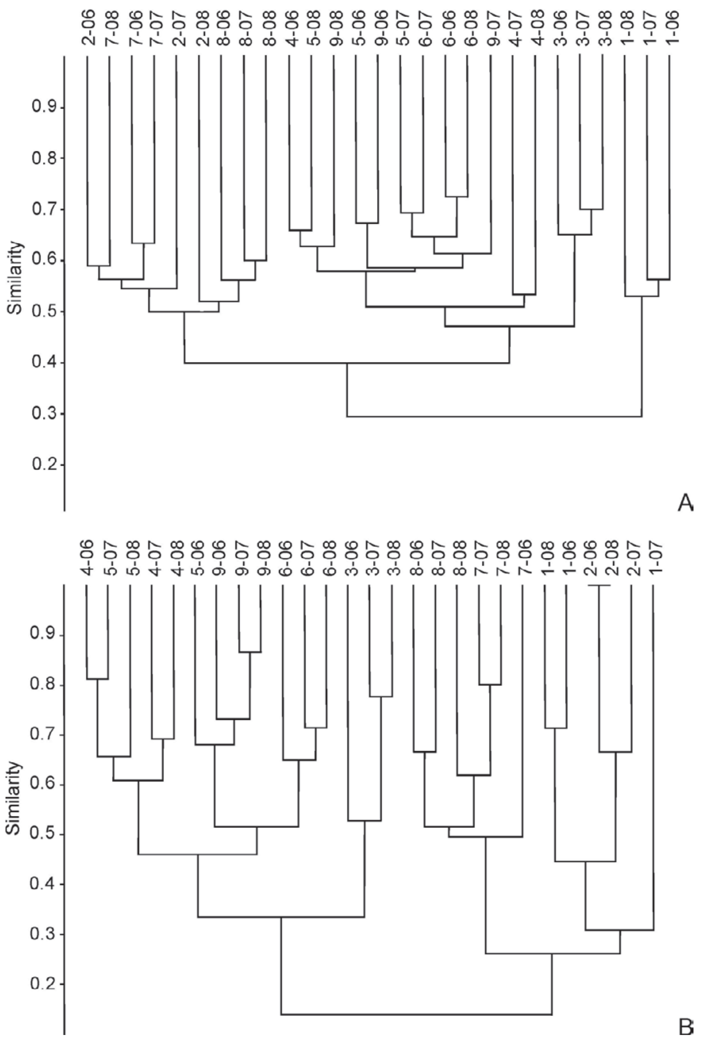

Figure 5. *Dendrograms of habitat similarity using Jaccard's coefficient, clustered using the UPGMA linkage method with consideration of the labile component (A) and of the residents alone (B). Habitats as in Table 2.*

of the total number of specimens (Fig. 6A). In the forest zone, elevations within inundated river flood-lands appear populated by many carabids to escape from, and to survive during the periods of, flooding, also used as their hibernating areas. Thus, the labile component is more diverse and abundant there at the beginning and end of the vegetation season. In the semi-desert zone, the species diversity and abundance of the stable component correlate negatively with habitat moisture. Migrants appear more diverse and abundant in riparian habitats (Fig. 6B). Due to a rather modest contrast between soil temperature and moisture as compared to dry open grasslands, meadow habitats offer relatively favourable conditions even during drier and hotter mid-summer months. As regards flood-plains, riparian habitats aid carabid migrations *(11, 12).*

Most species of ground beetles appear randomly distributed in the mosaic of a flood-plain landscape. Some of them inhabit the majority of habitats, while others reproduce only in a few types of meadow with specific soil-vegetation conditions. Annual variations in species diversity and abundance, due to changes in the environmental conditions, result from local migrations within a meta-population. The abundance of local populations of most of the stenotopic species is determined by their reproductive potential. Due to their narrow ecological ranges, these species are limited in potential habitats, and their residential habitats are few and often fragmentary *(55).* This increases the risk of their extinction, while a recovery of the abundance and complete demographic structure depends on large-scale migrations. In these cases, variations in abundance under sharp annual changes in the environmental conditions are characterized by maximum amplitudes. This seems to be accounted for both by poor immigrations from the adjacent habitats and poor fecundity rates in the local populations. For example, the abundance of *O. helopioides* both in residential and transit habitats remained virtually constant (Appendix). Nevertheless, a decline of the number of residential habitats

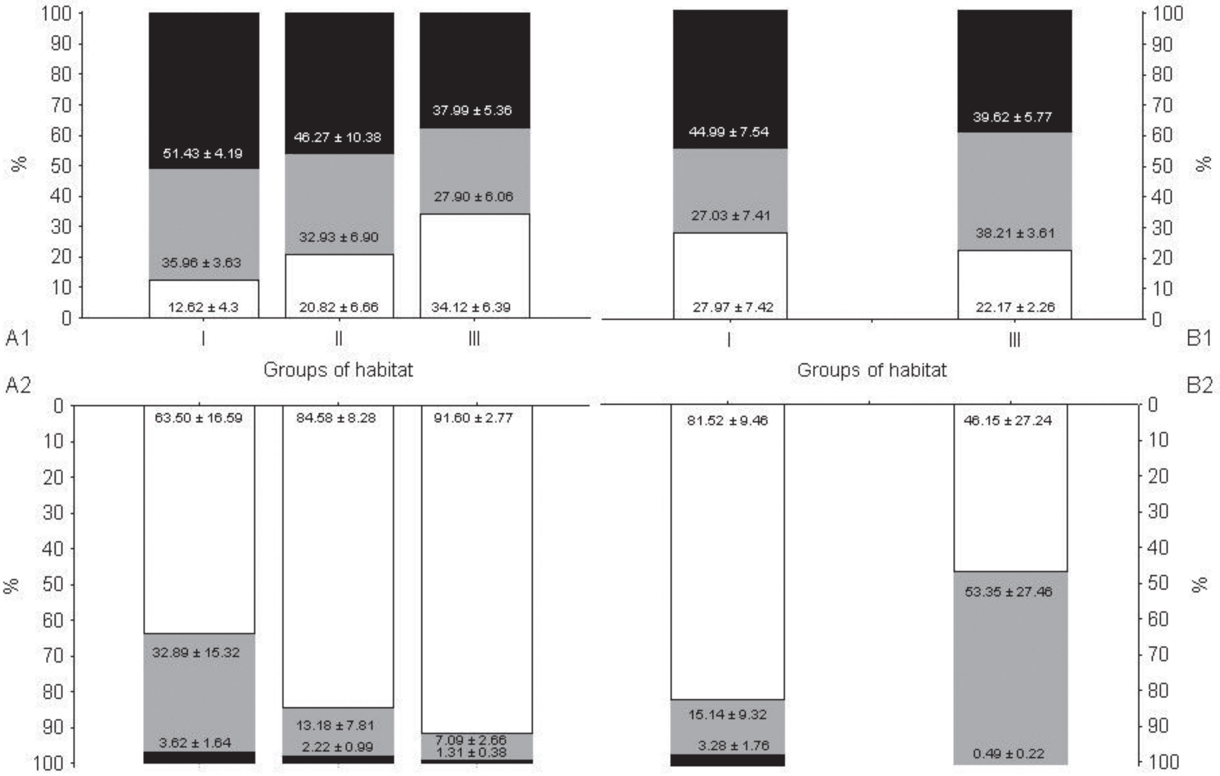

Figure 6. *The mean average proportions of stable and labile components in different groups of grassland habitats (A – Oka River valley, B – Elton Lake region, A1, B1 – species diversity, A2, B2 – species abundance, white boxes – resident species, grey boxes – migrants, black boxes – sporadic species, after ± the values of SD are given, groups of habitats as in the above text).*

during all three years from six to four, and a sharp increase in 2008 in the proportion of females of ancestral generations indicated non-optimal conditions in the local populations of this species. Thus, we believe that the reconstitution of the demographic structure of the local populations of stenotopic species takes place immediately after the living conditions are improved. However, for the recovery of the abundance to the initial population level, at least two, maybe even three years are required.

Eurytopic species are easy to redistribute and occupy all potential habitats available for breeding and development.

Immature and spent specimens of many spring-breeding carabids often move from lowland habitats to permanently dry flood-plain areas for hibernation *(56, 57)*. In such habitats, they are recorded at the end or beginning of the vegetation season. At the same time, the abundance of some species (*C. granulatus*, *O. helopioides*) can be quite high, dropping to just a few individuals in certain other species (*P. anthracinus*, *P. nigrita*, some *Bembidion*). Some species move into dry habitats to escape inundation. For example, the high abundance of *C. granulatus*, *B. gilvipes*, *A. fuliginosum* and *O. helopioides* in a dry forb-grass meadow with *Carex leporina* can be accounted for by the vicinity to lowland habitats. Those species were more numerous there only at the beginning of the vegetation season when most of the flood-plain was inundated, with mature specimens also prevailing.

The high abundance of the local populations of some Carabidae species was maintained not only by migrations, but also by life-cycle transformations. All local populations of *P. melanarius* and *H. rufipes* completed their annual life cycle in the cool and wet year 2006. However, in the dry and hot years 2007 and 2008, first facultative and then obligate-biennial life cycles were observed.

In 2006-2007, *P. melanarius* hibernated mostly as larvae, whereas in 2007, and especially in 2008, this species hibernated mostly as immature beetles *(10)*. Thus, its abundance levels in the residential habitats were maintained high throughout the years of our study (Appendix). For *P. melanarius* this seems to be especially important because of its limited migration capacities related to its inability to fly *(58, 59, 60)*. In *H. rufipes*, after changes in the environment, not only the duration of development was modified, but also the migration activity intensified. In particular, during 2007, seven of the nine flood-plain meadows were transit for this species, while the proportion of migratory specimens generally exceeded 80%. We believe that, under unfavorable environmental conditions, this species is capable of large-scale migrations in search of habitats suitable for breeding. This corresponds well with the high migration potential of *H. rufipes (58, 59, 60)*, as well as with the beetles' ability to move over long distances *(11, 61)*. The specimens hibernated both as larvae and as immature beetles, belonging to different generations, as a rule. The age heterogeneity of the local populations increases its stability, preventing abrupt changes in abundance and reducing the risk of extinction *(62, 63)*.

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APPENDIX

Species composition and abundance of species of Carabidae in study meadows in the Oka River valley

Group of habitats	I									II									III								
Habitats	1			2			8			7			4			5			6			9			3		
Species / Year	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
Cylindera (Cylindera) germanica					*1*			*1*							*1*		4		*1*								
Cicindela (Cicindela) campestris			*1*																								
Leistus ferrugineus		*1*																									
Notiophilus aquaticus				*1*																							
N. palustris											*1*										*1*						
N. germinyi				*2*			*1*		*2*			*1*															
Calosoma (Acalosoma) inquisitor									*1*																		
C. (Charmosta) investigator																			*2*		*2*						
Carabus (Eucarabus) stscheglovi				*1*	*1*	*2*				*10*	*5*	*4*	*8*	*3*	*6*	*6*	*8*	*26*	*6*	**41**	**40**	*16*	*32*	*28*			
C. (Tachypus) cancellatus				*3*			*1*	*1*		*7*	*1*		*33*	*4*	*15*	*3*	*6*	*10*	*2*	*9*	*22*	*4*	*7*	*10*			
C. (Carabus) granulatus	*2*	*1*	*1*	*108*	*41*	*18*	**354**	**71**	**35**	**219**	**83**	**28**	**305**	**94**	**61**	**247**	**281**	**276**	**233**	**207**	**145**	**333**	**483**	**282**	**88**	**235**	**330**
C. (C.) menetriesi																									**59**	**22**	**45**
C. (Trachycarabus) estreicheiri										*4*	*5*	*2*		*2*	*1*	*3*	*2*		*3*	**16**	**41**						
C. (Limnocarabus) clathratus				*4*	*3*	*1*				*9*		*4*	*4*	*1*	*4*	*1*		*1*	*5*	*2*	*2*	*2*	*1*	*2*			
C. (Megodontus) aurolimbatus											*1*	*1*	*15*	*6*	*19*	*3*	*4*	*1*	**23**	**17**	**88**	*3*	*8*	*6*			
Elaphrus (Neoelaphrus) cupreus																	*1*				*1*		*2*	*1*	*4*	*1*	
Loricera (Loricera) pilicornis										*1*		*1*	*2*		1		1		*10*	*1*	*1*	*1*	*2*		*27*	*3*	
Clivina fossor										*3*	*1*		*36*	*9*	*1*	**75**	**90**	**32**	**99**	**85**	**103**	**58**	**73**	**58**	*4*	*10*	*4*
Dyschirius (Dyschiriodes) tristis											*1*					*1*											
Trechus (Epaphius) rivularis					1									*2*											*2*	*8*	*2*
T. (E.) secalis		*1*	*1*	*41*	*6*	*4*	*2*	*12*	*17*	*4*	*5*	*1*	*2*	*8*	*6*		*16*	*10*	*3*	*8*	*10*		*2*	*3*	*1*	**164**	**117**
Asaphidion flavipes	*1*									*1*							*1*										
Bembidion (Metallina) lampros							*1*																				
B. (M.) properans	*1*						*2*			*6*	*2*		*2*											*1*			
B. (Eupetedromus) dentellum		*1*								*2*						*13*		*2*	*17*			*6*			*8*	*2*	*1*
B. (Philochtus) biguttatum		*1*		*6*	*2*				*2*	*6*	*6*	*3*	**62**	**25**		**31**	**34**	**51**	**76**	**88**	**71**	**15**	**56**	**30**	**46**	**64**	**90**
B. (Ph.) guttula		*1*		*7*	*1*	*2*	*2*	*2*	*1*	*17*	*8*	*4*	**86**	*18*	**51**	*1*	**28**	**36**	*3*	**63**	**31**	*1*	*10*	*10*		*19*	*9*
B. (Ph.) unicolor							*1*																			*1*	
B. (Leja) octomaculatum																				*1*							

Group of habitats	I									II									III								
Habitats	1			2			8			7			4			5			6			9			3		
Year Species	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
B. (*Trepanedoris*) *doris*					*1*												*1*		*2*			*1*	*1*		*9*	*3*	*1*
B. (*Semicampa*) *gilvipes*				*46*	*52*	*6*	*4*	*3*	*2*	*6*	*6*	*3*	**126**	**94**	**85**	**107**	**462**	**154**	**110**	**127**	**211**	**32**	**151**	**97**	**78**	**250**	**188**
B. (*Diplocampa*) *assimile*				*1*	*2*						*1*	*1*	*1*				*2*		**29**	*2*	**23**		*2*			*2*	
B. (*Bembidion*) *quadrimaculatum*				*1*													*1*										
Patrobus atrorufus		*1*		*2*	*7*						*7*	*1*		*2*		*10*	*2*		*1*	*6*	*1*	*19*	*10*	*4*	**33**	**71**	**25**
Poecilus (*Poecilus*) *cupreus*	*7*	*14*	*5*	*33*	*13*	*11*	*159*	**63**	*16*	**41**	*24*	*28*	**24**	*12*	*22*	**15**	**59**	*44*	**25**	**73**	*51*	*1*	*6*	*10*	*1*	**21**	*16*
P. (*P.*) *versicolor*	**207**	*32*	**37**	**587**	**203**	**741**	**1259**	**526**	**180**	**469**	**361**	**498**	**476**	**359**	**399**	**48**	**612**	**550**	**93**	**575**	**918**	*14*	**529**	**286**	*3*	**181**	**139**
P. (*P.*) *lepidus*	**43**	*30*	*45*	**80**	**29**	**88**	**65**	**75**	*167*	*10*	*13*	*11*			*1*												
Pterostichus (*Platysma*) *niger*			*1*	*4*			*6*	*2*	*1*	*2*	*10*	*1*	*6*	*16*	*14*	**21**	*9*	*60*	*6*	*12*	*2*	**43**	**39**	**74**	*10*	**26**	**56**
P. (*Argutor*) *chameleon*																			*2*		*2*			*1*			
P. (*A.*) *vernalis*	*1*	*1*		*8*	*4*	*5*	*1*	*4*		*2*	*6*	*9*	*8*	*4*	*5*	*7*	*3*	*16*	**37**	**41**	**186**	*8*	**29**	**24**		**29**	**32**
P. (*Pseudomaseus*) *anthracinus*	*4*	*5*	*6*	*18*	*12*	*10*	*9*	*22*	*10*	*32*	*43*	*20*	**70**	*13*	*10*	**258**	**72**	**110**	**303**	*30*	**248**	**208**	**117**	**114**	**228**	**108**	**93**
P. (*P.*) *gracilis*	*1*	*2*		*3*	*1*			*2*	*2*	*5*	*2*	*1*	*3*			*4*	*1*	*1*	*38*	*4*	*8*	*14*	*1*	*5*	*15*	*3*	*5*
P. (*P.*) *minor*		*1*			*1*			*8*	*2*	*1*	*2*			*1*		*2*	*1*		*8*	*3*	*1*	*1*	*8*		**29**	**30**	**33**
P. (*P.*) *nigrita*		*2*	*1*	*14*	*11*	*2*		*4*	*4*	*5*	*6*	*3*	*21*	*3*	*3*	*26*	*19*	*10*	**44**	**28**	**80**	**45**	**20**	**17**	**105**	**56**	**91**
P. (*Phonias*) *diligens*					*1*	*2*						*3*											*3*	*1*	*3*	**34**	**31**
P. (*Ph.*) *strenuus*				*5*	*15*	*4*	*1*	*7*	*2*	*2*	*1*	*10*	*2*	*8*	*17*	*1*	*3*	*3*		*2*	*3*		*24*	*6*		**54**	**17**
P. (*Ph.*) *taksonyis*				*1*																		*1*					
P. (*Bothriopterus*) *oblongopunctatus*					*1*		*2*	*1*																			
P. (*Morphnosoma*) *melanarius*	*1*			*18*	*2*	*5*	*63*	*30*	*8*	**282**	**597**	**279**	**194**	**350**	**612**	**319**	**552**	**683**	**94**	**411**	**573**	**112**	**834**	**447**	**95**	**402**	**199**
Calathus (*Calathus*) *fuscipes*	**15**	**78**	**118**	*6*	*2*	*4*	*4*	*6*	**50**	*2*	*1*																
C. (*Neocalathus*) *ambiguus*								*1*																			
C. (*N.*) *erratus*	*2*	*5*	*2*	*1*			*5*	*11*	**36**																		
C. (*N.*) *melanocephalus*	*10*	**28**	*5*	**58**	**42**	**38**	**65**	**40**	**101**	**22**	**30**	**95**	*8*	*22*	*6*		**19**		*1*	*36*	*73*		*6*	*1*		**16**	*1*
Dolichus halensis					*1*		*2*			*1*				*1*													
Agonum (*Platynomicrus*) *gracilipes*	*1*	*1*		*1*	*1*			*2*		*1*	*1*						*2*										
A. (*Agonum*) *duftschmidi*					*1*						*1*							*1*	*3*		*2*	*2*	*2*	*10*	*2*	*2*	*7*
A. (*A.*) *dolens*																*2*			*3*		*1*	*1*			*1*		*1*
A. (*A.*) *sexpunctatum*							*1*																		*1*		
A. (*A.*) *versutum*	*1*	*1*	*1*										*4*			*3*	*4*		*12*	*1*	*7*	**36**	*5*	*1*	**32**	*2*	*1*
A. (*A.*) *viduum*				*15*	*3*	*5*	*1*	*3*	*1*	*4*	*2*	*2*	*15*		*1*	**28**	*3*	**31**	**145**	*14*	**65**	**455**	**25**	**97**	**153**	**13**	**34**

Group of habitats	I									II									III								
Habitats	1			2			8			7			4			5			6			9			3		
Year Species	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
A. (*Europhilus*) *fuliginosum*				41	57	28	2	2	1	9	9	4	1			1	3	3	10	7	7	7	16	3	**32**	**33**	**30**
A. (*E.*) *gracile*				5	2	1		1			1					6				2	1	12		3	19	3	8
A. (*E.*) *micans*														1		3			11			4					
A. (*E.*) *piceum*																						6					
Platynus (*Platynus*) *assimile*																										4	
P. (*P.*) *krynickii*							7	7	3	1	2	1								1		1	1			**50**	**68**
P. (*Batenus*) *livens*																							1				
Oxypselaphus obscurus				1	1			4		1	2	2		2			1			4	4	2	1		**47**	**99**	**36**
Anchomenus (*Anchomenus*) *dorsalis*					2		10			1	2	1			1												
Olistophus rotundatus							1	1																			
Synuchus (*Synuchus*) *vivalis*	15	6	1	67	5		**54**	**20**	2	**37**	12	1	**17**	**57**		4	**97**		2	4	1	2	**13**			3	
Amara (*Zezea*) *plebeja*				2	1	4	3	3				5		1						1	5				1		
A. (*Amara*) *aenea*	15	13	19		1	4	82	62	42	8	16	5			1							1					
A. (*A.*) *communis*	8	5		37	7		27	15	12	18	13	38	15	**27**	**75**	1	**84**	5	2	**48**	16		3	3	1	**20**	6
A. (*A.*) *convexior*	2	3	1	1	1	2			1	1																	
A. (*A.*) *eurynota*									1																		
A. (*A.*) *famelica*				2																							
A. (*A.*) *familiaris*				1		1	18	1	3	14	2			1	1					1				1			
A. (*A.*) *littorea*												1															
A. (*A.*) *lunicollis*	1					4			1	9	19	**75**		1	19	3	82	4			2						
A. (*A.*) *nitida*	1											1		1													
A. (*A.*) *ovata*				1	1	1	23	22	3	2	12	1			1									1			
A. (*A.*) *similata*			1				4			1		1		2			1		1	2							
A. (*A.*) *tibialis*			6	2	5	15	19	6	6	5	1	2															
A. (*Celia*) *bifrons*	2	1	15				**32**			1																	
A. (*Bradytus*) *apricaria*										1																1	
A. (*B.*) *consularis*	7		3						1																		
A. (*Percosia*) *equestris*	**13**	**79**	**55**	**29**	**85**	**34**	**44**	**148**	**214**	9	**38**	**26**	1														
A. (*Curtonotus*) *aulicus*				1				1			3	1	1	1			1						1				
Anisodactylus (*Anisodactylus*) *binotatus*			1		1		1	1			2			2					1	1	1						
A. (*A.*) *nemorivagus*	10	17	5		1	1	6	22	3	2																1	

Group of habitats	I									II									III								
Habitats	1			2			8			7			4			5			6			9			3		
Species / Year	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
A. (Pseudanisodactylus) signatus			2				3	1	1	2				1										2			
Bradicellus (Bradicellus) caucasicus		1			3	1														1							
Dicheirotrichus (Trichocellus) cognatus														1													
D. (T.) placidus																	2			1							1
Stenolophus (Stenolophus) mixtus							1			2	2							2	6		1					1	
Acupalpus (Acupalpus) meridianus										1	1												1			1	
A. (A.) exiguus				5	5	2	1	3	1	1	10	1	14	5		14	6	8	16	**42**	**106**	1	23	19	6	**24**	**56**
Anthracus consputus														1													
Harpalus (Pseudophonus) calceatus		1				1			2																		
H. (P.) griseus		5						3	1		1			1			1			2						1	
H. (P.) rufipes	**90**	70	**126**	**124**	147	**159**	**635**	416	**388**	**634**	215	**201**	**226**	**121**	**127**	**314**	**85**	39	29	17	8	15	14	9	11	12	8
H. (Semiophonus) signaticornis		1				1		3																		1	
H. (Harpalus) rubripes	35	28	**29**	**91**	19	**46**	13	27	13	1	3		1	1						1	3					2	2
H. (H.) pumilus			1			1																					
H. (H.) anxius	1		5						3			1															
H. (H.) tardus	4	10	17	2		2	2	5	8	1		1															
H. (H.) latus	5	8	11	31	4	4	**52**	**26**	**163**	**149**	**66**	**79**	**141**	**81**	**82**	**62**	**239**	**85**	43	**101**	**65**	20	**53**	**67**	10	**34**	7
H. (H.) luteicornis	10	12	16	3	3	8	**171**	**379**	**312**	**81**	**36**	**47**	6	**25**	14	1	6		1	4	3					1	1
H. (H.) smaragdinus	**48**	12	**57**	2		2	1	2	1		1																
H. (H.) affinis	36	12	17			1	**45**	16	22	4	2																
H. (H.) distinguendus	2	2	1	2	1	1	5	2	1	4	2	2															
Ophonus (Metophonus) puncticollis			1			1																					
O. (M.) rufibarbis							1																				
O. (Ophonus) stictus	2	2		1																							
O. (Hesperophonus) azureus	1							2	1																		
Panagaeus (Panagaeus) cruxmajor				1	22	1				9	18	7	5	5	6	1	6	2	6	8	**16**		13	13	2	10	2
P. (P.) bipustulatus	3	1	3	1		3	8	12	4	**20**	13	1	1	3	2			1									
Callistus lunatus							1		1																		
Chlaenius (Chlaenius) nigricornis	1			2			2			12	3	3	6	1		12	6	7	8	2	6	8	2	4	4	4	5
Ch. (Ch.) tristis																											1

Group of habitats	I									II									III								
Habitats	1			2			8			7			4			5			6			9			3		
Species / Year	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008	2006	2007	2008
Ch. (*Pelasmus*) *costulatus*															*1*												
Oodes (*Oodes*) *helopioides*		*1*		*149*	*27*	*110*	*6*	*11*	*3*	**93**	*44*	*29*	**164**	**60**	*32*	**140**	**110**	**146**	**247**	**94**	**382**	**450**	**243**	**183**	**331**	**306**	**544**
Licinus (*Licinus*) *depressus*	*2*	*1*	*8*	*15*	*10*	*17*	*3*	*4*	*8*	*3*	*4*	*2*	*3*	*3*	*3*		*2*			*3*	*1*	*1*	*3*	*4*			
Badister (*Badister*) *bullatus*				*4*		*1*	*1*		*1*	*1*																	
B. (*B.*) *unipustulatus*				*2*							*1*	*1*						*1*						*1*	*13*	*5*	*4*
B. (*Trimorphus*) *dorsiger*																							*3*		*1*	**25**	*17*
B. (*T.*) *sodalis*				*1*		*1*			*1*		*3*	*1*											*2*	*2*	*3*	**17**	*4*
B. (*Baudia*) *dilatatus*				*1*								*1*									*1*				*11*		
B. (*B.*) *peltatus*											*1*									*4*			*1*		*1*	*1*	
Masoreus wetterhalli		*1*																									
Odacantha (*Odacantha*) *melanura*											*1*														*1*		
Lebia (*Lamprias*) *chlorocephala*				*1*				*2*						*2*													
L. (*Lebia*) *cruxminor*								*1*																			
Demetrias (*Demetrias*) *monostigma*																										*1*	
Paradromius (*Manodromius*) *linearis*				*1*	*2*			*1*																			
Philorhizus sigma													*1*	*1*	*1*		*1*	*2*		*1*	*1*		*1*			*2*	
Syntomus truncatellus				*4*	*2*			*2*						*1*													
Microlestes maurus	*4*	*1*	*3*			*2*		*1*	*1*		*1*			*1*	*2*					*1*							
M. minutulus				*1*	*1*				*3*		*1*																
Cymindis (*Cymindis*) *angularis*	*1*			*1*		*1*		*9*	*10*																		
Brachinus krynickii				*43*	*10*	*6*				**31**	**29**	**29**	**32**	**19**	**22**	*1*	**47**	**121**		*2*		*10*	*32*	**93**			
Number of species:																											
residents	6	3	6	6	4	6	11	9	9	12	8	10	13	12	10	13	16	12	14	17	19	12	14	14	14	27	21
migrants	14	17	14	26	21	20	20	24	16	25	25	14	16	13	15	10	13	12	16	15	12	13	15	14	14	7	13
sporadic	21	25	18	34	33	26	27	29	33	28	36	34	13	29	16	17	22	12	17	22	22	17	21	16	15	23	11
Total		63			86			86			89			68			61			67			63			64	
Abandance:																											
residents	416	185	422	969	359	1106	2776	1348	1479	2078	1240	1357	1923	1312	1537	1665	2871	2275	1558	2057	3392	1801	2665	1869	1356	2384	2254
migrants	170	284	180	734	479	272	478	742	350	226	529	178	204	130	195	102	176	239	231	167	217	143	214	138	151	68	100
sporadic	30	31	26	50	49	37	41	51	53	41	56	50	21	44	22	31	36	20	33	34	34	28	36	27	24	42	14

Notes: **bold** – residents, *italic* – migrants, *underlined italic* – sporadic species.