Biosozologia, Bratislava, 4: 34–44, 2006

Shifts in habitat preference of some montane Carabid beetles and their possible causes

Zbyšek Šustek

Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, SK–845 06 Bratislava, Slovakia; e-mail: zbysek.sustek@savba.sk

ŠUSTEK, Z., Changes in habitat preference of some montane Carabid beetles and their possible causes. Biosozologia, Bratislava, 4: 34–44, ISBN

Abstract: The submontane and montane Carabid communities consist predominantly of the species showing, in lower altitudes (vegetation tiers), a strong preference for habitats with close tree cover. Deforestation results, under such conditions, in a strong drop of abundance of these species. On the contrary, in higher altitudes, some of these species (especially *Pterostichus pilosus, Pterostichus foveolatus, Calathus metallicus*) lose this preference and also reach high abundances in subalpine meadows. The cause of this habitat preference shift is the highly positive climatic water balance in these habitats. The climatic water balance seems to be a better characteristic of habitat humidity than pure annual precipitation.

Key words: Carabid beetles, habitat preference, climatic water balance

Introduction

The montane Carabid fauna in Central Europe consists almost completely of species which are characterized as forest species, i. e. those species which require or, at least, prefer habitats permanently shaded by a closed tree vegetation (BURMEISTER, 1939, THIELE 1977, HŮRKA 1996, ŠUSTEK 2000, CRISTAND-PESKOLLER et JANETSCHEK 1976, DE ZORDO 1979, GROSSENSCHALAU 1981). This habitat preference is a logical consequence of the fact that in the past major part of natural Central European landscape was almost completely covered by closed climax forest. In the submontane and montane conditions, the open, non-forest, areas permanently existed only on steep rock slopes. Temporarily they also arose, due to natural disturbances and catastrophes, in other places, but such areas never were extensive and succession of their vegetation cover always tended to restore a state corresponding to the potential vegetation that was characteristic of the respective ecotope. The permanent natural non-forest vegetation – alpine or subalpine meadows – is limited only to high altitudes, above the limit of natural distribution

Tab. 1. **Changes in abundance of Carabids along a transect crossing an avalanche scar in Jamborová dolina in State Nature reserve Šrámková in Malá Fatra Mts.**
(D – dominance of abundance, numbers of traps correspond to ŠUSTEK et ŽUFFA 1986)

Species	Trap number											Total	Mean	D %
	Forest					Scar		Forest						
	1	2	3	4	5	6	7	8	9	10	11			
Abax parallelepippedus (PILLER et MITTERPACHER,1783)	17	29	38	47	21	4	6	34	20	29	40	285	25.91	26.51
Abax ovalis (DUFTSCHMIDT,1812)			3	2			2	13	3		4	27	2.45	2.51
Bembidion deletum AUDINET-SERVILLE,1821					4							4	0.36	0.37
Cychrus attenuatus (FABRICIUS,1792)		1	3	1				1			7	13	1.18	1.21
Cychrus caraboides (LINNAEUS,1758)				1								1	0.09	0.09
Carabus coriaceus LINNAEUS,1758		1	2	1	1		7	5	4	2	1	24	2.18	2.23
Carabus irregularis FABRICIUS,1792	1	2	3		3	3					2	14	1.27	1.30
Carabus linnei PANZER,1810	1	3		5							3	12	1.09	1.12
Carabus obsoletus HERBST,1764	4	4	3	19	22	4	5	30	12	8		111	10.09	10.33
Carabus scheidleri PANZER,1799	1			2	8	1	5		6	1	1	25	2.27	2.33
Carabus sylvestris PANZER,1796											1	1	0.09	0.09
Carabus irregularis FABRICIUS,1792	1	2	5	7	13		13	4	5	10	6	66	6.00	6.14
Molops piceus (PANZER,1793)		3		4	2						7	16	1.45	1.49
Pterostichus burmeisteri HEER,1841	1	1	8	19	7	2	4	12	7	1	2	64	5.82	5.95
Ptrerostichus niger (SCHALLER,1783)					5		1	1				7	0.64	0.65
Pterostichus pilosus (HOST,1789)	25	6	21	16	9	2		7	6	6	13	111	10.09	10.33
Pterostichus unctulatus (DUFTSCHMIDT,1812)			3	11								14	1.27	1.30
Pterostichus foveolatus (DUFTSCHMIDT,1812)	18	11	16	42	17	6	4	14	18	14	36	196	17.82	18.23
Trichotichnus laevicollis (DUFTSCHMIDT,1812)		7			6	5	9		1			28	2.55	2.60
Trechus latus PUTZEYS,1847											1	1	0.09	0.09
Trechus pilisensis CSIKI,1918					3							3	0.27	0.28
Trechus pulchellus PUTZEYS,1846	3	3	2	1		4		25		4	10	52	4.73	4.84
Number of individuals	72	73	107	178	121	31	56	146	82	75	134	1075	179.17	
Number of species	10	13	12	15	14	9	10	11	10	9	15	22		

Tab. 2. **Changes in abundance of Carabids along a transect crossing a small meadow in forest on the hills Žobrák I and Žobrák II in the state State Nature Reserve Šrámková in Malá Fatra Mts.**
(D – dominance of abundance, numbers of traps correspond to ŠUSTEK et ŽUFA 1986)

Species	Trap number											Total	Mean	D %
	Forest					Meadow			Forest					
	17	18	19	20	21	22	23	24	25	26	27			
Pterostichus pilosus (HOST,1789)	13	43	11	44	3	1	2	19	95	94	89	414	37.64	24.91
Pterostichus unctulatus (DUFTSCHMIDT,1812)	24	26	49	14	25	7	1	9	11	14	19	199	18.09	11.97
Trechus pulchellus PUTZEYS,1846	19	8	40	16	15	10	43	5	2	2		160	14.55	9.63
Calathus metallicus DEJEAN,1828	6	19	41	25	13	4	4	6	11	16	13	158	14.36	9.51
Pterostichus foveolatus (DUFTSCHMIDT,1812)	1	9	10	7	2	1	3		28	38	48	147	13.36	8.84
Trichotichnus laevicollis (DUFTSCHMIDT,1812)	5	5	7	8	8	2		6	10	17	8	76	6.91	4.57
Carabus arcensis HERBST,1784	57	8		1	4		1					71	6.45	4.27
Carabus linnei PANZER,1810	7	7	5	3				3	2	6	2	35	3.18	2.11
Carabus irregularis FABRICIUS,1792		1		1				3	8	10	11	34	3.09	2.05
Carabus violaceus LINNAEUS,1758	8	1		1		2		1	4	2	7	26	2.36	1.56
Trechus pilisensis CSIKI,1918		4	2	3	1			1	3	4	4	22	2.00	1.32
Trechus latus PUTZEYS,1847			8	4						2	3	17	1.55	1.02
Cychrus caraboides (LINNAEUS,1758)	3	3			1				2	2	4	15	1.36	0.90
Pterostichus burmeisteri HEER,1841		2						1	7	2	1	13	1.18	0.78
Pterostichus strenuus (PANZER,1797)					7	2	1					10	0.91	0.60
Pterostichus pumilio (DEJEAN,1828)			3	1	2	1	1					8	0.73	0.48
Cychrus attenuatus (FABRICIUS,1792)		1	3	1							2	7	0.64	0.42
Notiophilus biguttatus (FABRICIUS,1779)						3						3	0.27	0.18
Carabus coriaceus LINNAEUS,1758									1			1	0.09	0.06
Pterostichus ovoideus (STURM,1824)			1									1	0.09	0.06
Carabus glabratus PAYKULL,1790			1									1	0.09	0.06

Pterostichus oblongopunctatus (FABRICIUS,1787)								1				1	0.09	0.06
Carabus auronitens FABRICIUS,1792											1	1	0.09	0.06
Number of individuals	160	155	200	149	102	55	79	79	209	235	239	1662	151.09	
Number of species	10	14	13	14	11	10	8	11	13	13	14	23		

of trees (timber line) and high shrubs (dwarf pine stands) (RAUŠER et ZLATNÍK 1966, ZLATNÍK 1976).

The vertical distribution of most species constituting the montane Carabid fauna is not, however, limited only to the highest altitudes. Almost all of them, more or less, descend to lower altitudes and also successfully live in the submontane forests, where they represent dominant or subdominant components of Carabid communities.

The earlier studies of Carabid communities made in the submontane or montane forests of the beech to spruce-beech-fire vegetation tiers (RAUŠER et ZLATNÍK 1966) in Central Bohemia (ŠUSTEK 1984a, b) and in the Malá Fatra Mountains (ŠUSTEK et ŽUFFA 1986, 1988) have confirmed that any kind of temporary or permanent removal of tree vegetation (clear-cutting, gale disasters, avalanche scars, transformation of forests into permanent pastures) results in almost total disappearance of the typical forests species not only from the affected site, but also from the insolated part of the adjacent forest stand (ŠUSTEK 1984a, b). According to local conditions, these species are gradually replaced by s.c. open landscape species and/or eurytopic species (in lower altitudes) or (in higher altitudes) in emerging of poor communities consisting of a small number of occasionally migrating individuals (metapopulations) of the forest species inhabiting adjacent intact parts of forests stands.

The studies made in 2004 – 2006 (ŠUSTEK 2006) in different types of natural ecosystems in spruce to alpine vegetation tiers in High Tatra and Belianske Tatry Mountains have shown that in subalpine and alpine conditions some species considered conventionally as stenotopic forest species change their habitat preference and life stra-tegy in habitats, where the tree vegetation does not exist naturally. The aim of this paper is to describe and explain these changes.

Material and methods

The beetles were collected by pitfall traps filled with 4% formaldehyde as conservation solution. In the earlier studies (ŠUSTEK et ŽUFFA 1986, 1988), the 0.75 l Omnia glass jars (opening diameter of 80 mm) buried in the soil served as traps, while in the present study in High Tatras the 0.50 l plastic glasses were used (opening diameter of 90. In the earlier studies the pitfall traps were set in lines crossing different habitats, while in the present study they were laid in lines in the center of the selected habitats. In the earlier studies, distance distances between traps and their number varied in a way making possible to characterize the ecological gradients studied (for details see ŠUSTEK et ŽUFFA 1986, 1988 or study), while in Belianske Tatry Mountains six traps were in each site at mutual distances of 10 m. The traps were exposed during whole vegetation season (in Belianske Tatry from the beginning of June to end of September) and emptied monthly.

Individual sampling sites in the Malá Fatra mountains were localized according to map in the scale of 1:10,000, while in Belianske Tatry by GPS. Vegetation in the habitats studied is characterized by the phytocoenological units (groups of types of geobiocoens, trophical rows and vegetation tiers) of the Zlatník's geobiocoenological system (RAUŠER et ZLATNÍK 1966, ZLATNÍK 1976, RANDUŠKA et al. 1986). The beetle nomenclature is adopted according to HŮRKA (1996). The activity abundance of species (size of the catch in indidindividual traps) is taken as a measure of habitat preference.

Study sites

1. Malá Fatra, Jamborová dolina – herbage vegetation in an avalanche scar (about 100 m wide) surrounded from one side by a mature stand of the geobiocoens group *Fagi Acereta* (beech-fire vegetation tier, trophic series BC [neutral-nutrophilous]) while by a young stand of the same group of geobiocoens from other side (altitude 950 – 1000 m). Samples from a 300 m long line of 7 traps crossing the scar and adjacent intact stands are selected in this study. Sampling was carried out in 1982 (ŠUSTEK et ŽUFFA 1986).

2. Malá Fatra, Šrámková – a transect crossing a sparse and low stand of the geobiocoens group *Piceeta Abietina* (beech fire vegetation tier, trophic row A) situated on the northern slope of the Žebrák II hill, passing through a slightly southerly exposed meadow in the saddle between the hills Žobrák I and Žobrák II end ending in mature stand of *Fagi Acereta* (spruce-beech-tire vegetation tier, trophic series BC [neutral-nutrophilous]) on the southern slope of the Žobrák II hill (altitude 1100 – 1300 m). Samples from a 600 long line of 11 traps are used in this study. Sampling was carried out in 1982 (ŠUSTEK et ŽUFFA 1986).

3. Malá Fatra, Kľačianska Magura, - a small meadow (about 100 x 200 mm) surrounded by a natural stand of the geobiocoens group *Fagi Abieta superiora* (spruce-beech-fire vegetation tier, trophic series AB [acidiphilous – neutral], altitude 1150 m) on southeastern slope of the Svrčiník hill. Samples from a 400 m long line of 7 traps crossing the meadow and the adjacent forests are used for comparison. Sampling was carried out in 1984 (ŠUSTEK et ŽUFFA 1988).

4. Malá Fatra, Kľačianska Magura, Svrčiník hill – a partly overgrown gale-disaster area (about 150 m in diameter) surrounded by a natural stand of the geobiocoens group *Aceri Piceeta* (spruce vegetation tier, throphic row A – AB [acidiphilous-neutral], altitude 1310 – 1330 m) gradually turning into a stand of the group of geobiocoens *Fagi Acereta* (spruce vegetation tier, throphic series BC, altitude about 1280 m). Samples from a 400 m long line of 5 traps crossing the damaged stand and the adjacent forest are used in this paper. Sampling was carried out in 1984 (ŠUSTEK et ŽUFFA 1988).

5. Belianske Tatry, Zadné Meďodoly – spruce white beam stand with admixed dwarf pines - the geobiocoens group *Sorbi-Piceeta* (spruce vegetation tier, throphic series BD [neutral-calciphilous], altitude 1585 m 20°12'26,1" N, 49°14'06,6" E) on the southwestern slope under the Hlúpy hill. Samples from a 50 m long line of 6 traps are used here. Samples from 2004 were used (ŠUSTEK 2006).

6. Belianske Tatry, a slope above Koptské sedlo saddle – a large plot of rich subalpine herbage vegetation with small dispersed groups of dwarf pines (dwarf pine vegetation tier, trophic series BD [neutral-calciphilous], altitude 1920 m, 20°13'07,0" N, 49°14'01,4" E) on the southern slope of the Hlúpy hill. Samples from 2004 were used (ŠUSTEK 2006).

Results and discussion

In the stands bordering the avalanche scar (Tab. 1), the dominant species have approximately the same abundance on both sides of the scar. The small differences can be interpreted as consequence of species competition etc. However, in all dominant species, in particular in *P. pillosus* and *P. foveolatus*, the abundance in the avalanche scar (traps 6 and 7) drops to about 10% of its values in the adjacent forests.

When compared with the precedent example, the transect crossing the meadow between the hills Žobrák I and Žobrák II characterizes a very complex ecological gradient (Tab. 2). That part, which was grown by an acidiphilous community *Piceeta Abietina*, was characterized first of all by an increased abundance of *P. unctulatus*, *T. pulchellus* and, to certain degree, also that of *C. metallicus* and by a local concentration of *C. arcensis*. The part grown by a nitro- and calciphilous community of a mature stand of *Fagi Acereta* was characterized by an increased abundance of *P. foveolatus*, *T. laevicollis* and *C. irregularis*. In both stands *P. pilossus* took position of an eudominand species. The limited trophicity of *Piceeta Abietina* was reflected by a smaller cumulative abundance of all Carabids (149 – 200 individuals) and predominance of small sized species (*T. pulchellus*, *P. unctulatus*), whereas the cumulative abundance of Carabids in *Fagi Acereta* exceeded 200 individuals (except of the trap 24 at the stand margin) and medium and large sized species predominated there (Tab. 2). In spite of complexity of the gradient, *P. pilosus* and *P. foveolatus* showed an obvious sudden drop in number of individuals in the three traps (21 – 23) situated in the meadow, as well as at the southern margin of the beech-maple stand. A smaller decrease could be also observed in *C. metallicus*, *P. unctulatus*, as well as in the cumulative abundance of all Carabids. The only species which did not respond to absence of tree cover was *T. pulchellus*.

The transect crossing a small gale disaster area in Klačianská Magura (Tab. 3, traps 12 – 18) formed a complex ecological gradient similar to that in Žebrák I and Žebrák II. The first two traps (13 – 14) were situated in the acidiphilous *Aceri Piceeta*, while two last traps (16 – 17) in a transition to the richer *Fagi Acereta*). Due to this, when compared with the traps 16 and 17, the cumulative abundance of Carabidae was smaller in the traps 13 – 14. Abundance of *P. pilosus*, *P. foveolatus* and *C. metallicus* was also lower here, but in contrast, the small sized *T. pulchellus* predominated here. In the center of gale disaster area (trap 15), a decrease in abundance was obvious in *P. pillosus*, *C. metallicus* and partly in *P. foveolatus*. On the contrary, *T. pulchellus* and *P. pumilio* did not show any visible response to the local damage of the forest stand.

In the continuation of this transect, which crossed a small meadow (Tab. 3, traps 25 – 29), a decrease in abundance could be seen in *P. pilosus* and *P. foveolatus*, similarly as in the previous cases. In contrast to them, *C. metallicus* did not show any visible change, but abundance of *T. pulchellus* dropped strongly.

A quite different situation was observed in two physiognomicaly strongly different communities in the Belianske Tatry Mountains (Tab. 4 and 5). As in an almost closed stand of spruce whitebeam stand with admixed dwarf pines, situated near to the timber line, as in a fully open grassy growth with thinly dispersed small islands of dwarf pine all species occurring here, inclusively of *P. foveolatus* and *P. pilosus*, showed a high abundance comparable with their abundance in the closed forest stands in lower altitudes (vegetation tiers) in all three localities of Malá Fatra (Tab. 1 – 3) and a homogenous distribution along the short transects. In addition, abundance of *P. foveolatus* and

Tab. 3. Changes in abundance of Carabids along a transect crossing a small reserve Kľačianska Magura in Malá Fatra Mts. (D – dominance of abun

Species	Trap number						
	Forest			Damaged	Forest		
	12	13	14	15	16	17	18
Trechus pulchellus PUTZYES,1846	273	124	47	111	186	113	297
Calathus metallicus DEJEAN,1828	78	42	31	13	44	58	135
Pterostichus unctulatus (DUFTSCHMIDT,1812)	30	144	4	15	28	20	17
Pterostichus pilosus (HOST,1789)	4	4	17	5	11	49	9
Pterostichus foveolatus (DUFTSCHMIDT,1812)	5	5	6	4	6	21	14
Pterostichus pumilio (DEJEAN,1828)	1	3	5	4	11	8	
Trechus pilisensis CSIKI 1917					2	3	2
Trichotichnus laevicollis DUFTSCHMIDT,1812			3	1	3	6	2
Carabus linnei PANZER 1813	2	2		2	5	3	2
Carabus arcensis HERBST,1784		2	4	4			
Carabus violaceus LINNAEUS,1758		1	2	1	1	1	
Cychrus caraboides (LINNAEUS,1758)				1	1	2	1
Cychrus attenuatus (FABRICIUS,1792)						1	
Carabus glabratus PAYKULL,1790							
Trechus latus PUTZEYS,1847	1						
Carabus auronitens LINNAEUS,1792							
Amara curta DEJEAN,1828							
Pterostichus strenuus (PUTZEYS,1797)						1	
Number of individuals	394	327	119	161	298	286	479
Number of species	8	9	9	11	11	13	9

P. pilosus in the subalpine grassy stand was even higher that in the closed sprucewhitebeam stand situated in a much lower altitude and in comparably favorable trophic conditions (neutral – calciphilous trohpical series BD).

The last two cases indicate that *P. pilosus* and *P. foveolatus* and, to certain degree, also *C. metallicus,* strongly change their close dependence on presence of tree cover in higher vegetation tiers. Because these species do not penetrate into the alpine vegetation tier (in study plots in the alpine vegetation tier they were replaced by the pair of codominant species *Pterostichus morio carpathicus* KULT, 1944 and *Pterostichus blandulus* MÜLLER, 1899 (ŠUSTEK 2006), it is excluded that this change in habitat preference could be caused by preference for lower temperature in higher altitudes. As the most probable factor making possible this different relationship to tree cover in these species seems the humidity. According to CHOMICZ et ŠAMAJ (1974) and ŠAMAJ (1978) the annual precipitation in the areas corresponding with the beech-fire to spruce-beech-fire vegetation tiers, in which *P. pillosus, P. foveolatus, C. metallicus* and other forest Carabids obviously prefer the mature forest stands and any kind of deforestation results in a sudden drop in their abundance, amounts about 800 – 1000 mm. In contrast, in the spruce vegetation tier, where the difference in abundance of these species in the forest

gale disaster area and small meadow in forest in the State Nature
dance, numbers of traps correspond to ŠUSTEK et ŽUFA 1988)

Forest		Meadow	Forest		Total	Mean	D %
25	26	27	28	29			
20	38	4	15	122	1350	112.50	51.43
25	20	29	38	50	563	46.92	21.45
12	13	14	30	12	339	28.25	12.91
12	13		2	15	141	11.75	5.37
2	3	1	1	7	75	6.25	2.86
2	1	4	5	1	45	3.75	1.71
5	6		16	2	36	3.00	1.37
	1		6		22	1.83	0.84
1	1	2			20	1.67	0.76
					10	0.83	0.38
			1		7	0.58	0.27
					5	0.42	0.19
1	1	1			4	0.33	0.15
			3		3	0.25	0.11
	1				2	0.17	0.08
1					1	0.08	0.04
			1		1	0.08	0.04
					1	0.08	0.04
81	98	55	118	209	2625	218.75	
10	11	7	11	7			

and deforested areas was lower (Tab. 4), the annual precipitation varies between 1500 and 1700 mm, whereas in the dwarf pine vegetation tier, where these species did not distinguish-between closed forest stand and subalpine meadows (Tab. 5), the annual precipitation exceeds 2000 mm. In spite of the fact that annual precipitation can be taken as a good characteristics of differences in habitat properties, ŠKVARENINA et al. (2002) have shown that a much better characteristic is the climatic water balance. These authors have shown that in individual month of growing season the potential evaporation considerably exceeds precipitation in oak or beech-oak vegetation tiers (PE = 130 mm, P = 50 – 60 mm equal (about 60 mm in spring and autumn). In the beech vegetation tier values of both parameters become approximately equal and towards the higher vegetation tier the precipitation start to exceed the potential evaporation. In the dwarf pine and alpine vegetation tiers the monthly climatic water balance becomes highly positive, the precipitation being already twice (in spring and autumn PE 80 – 100 mm, P 40 – 50 mm) to three – four times higher (in summer PE 50 – 60 mm, P 180 – 200 mm) than potential evaporation.

The influence of higher humidity expressed by the positive climatic water balance in higher vegetation tiers is also reflected in diurnal activity of Carabids. In lower vegeta-

Tab. 4. Changes in abundance of Carabids along transect of six traps in a homogeneous spruce white beam stand with admixed dwarf pines in State Natue Reserve Zadné Meďodoly in Belianske Tatry Mts.
(D – dominance of abundance)

Species	Trap number						Total	Mean	D %
	1	2	3	4	5	6			
Pterostichus foveolatus (DUFTSCHMIDT,1812)	17	22	18	21	26	19	123	20.50	45.90
Calathus metallicus DEJEAN, 1828	12	9	7	11	16	13	68	11.33	25.37
Pterostichus pilosus (HOST,1789)	4	1	3	1	4	3	16	2.67	5.97
Trechus striatulus (PUTZEYS,1847)	3	1	2	4	2	3	15	2.50	5.60
Cychrus attenuatus (FABRICIUS,1792)	2	5	3	2	1	2	15	2.50	5.60
Pterostichus unctulatus (DUFTSCHMIDT,1812)		1	2	1	2	2	8	1.33	2.99
Leistus piceus FROELICH,1799	1	1		2		2	6	1.00	2.24
Carabus linnei PANZER, 1810			1		1	2	4	0.67	1.49
Carabus violaceus LINNAEUS, 1758	1		1	1			3	0.50	1.12
Trichotichnus laevicollis (DUFTSCHMIDT, 1812)			1		1	1	3	0.50	1.12
Cychrus caraboides (LINNAEUS, 1758)	1					1	2	0.33	0.75
Pterostichus pumilio (DEJEAN, 1828)	1		1				2	0.33	0.75
Calathus micropterus (DUFTSCHMIDT,1812)		1		1			2	0.33	0.75
Carabus auronitens FABRICIUS,1792	1						1	0.17	0.37
Number of individuals	43	41	39	44	53	48	268	44.67	
Number of species	10	8	10	9	8	10	14		

tion tiers they are mostly active at night, when the humidity is larger, while in the higher vegetation tiers they can be also day active, even in warm sunny days, due higher humidity.

A similar shift in habitat preference of Carabids can be also observed in lower vegetation tiers, particularly in the thermoxerophilous steppe-like habitats of degradation stages of *Corni Querceta* (ŠUSTEK 2004) in oak vegetation tier. In these habitats, the forest Carabids inhabiting the adjacent forest stand appear only in late autumn or early in the spring, when – according to ŠKVARENINA et al. (2002) – the potential evaporation is approximately equal with precipitation. Similar phenomena can be observed also in distribution of forest Carabids along different wind-breaks and other line formation of tree vegetation (ŠUSTEK 2002). Also these examples show the climatic water balance to be a suitable characteristic of habitat humidity and habitat preference of animal species.

Conclusions

The observations made along the range of vertical distribution of some Carabid beetles show, that the montane species *P. pillosus* and *P. foveolatus* change their ecological requirements only apparently. They constantly require a high humidity expressed as positive climatic balance. In lower altitudes (lower vegetation tiers in sense of RAUŠER et ZLATNÍK 1966) these requirements are satisfied only in fully closed forest stands where, similarly as as in higher altitudes, their humidity requirements can be also satis-

Tab. 5. Changes in abundance of Carabids along transtect of six traps in a large plot of rich subalpine herbage vegetation with small dispersed groups of dwarf pines in State Nature Reserve Zadné Meďodoly in Belianske Tatry Mts.
(D – dominance of abundance)

Species	Trap number						Sum	Mean	D %
	1	2	3	4	5	6			
Pterostichus foveolatus (DUFTSCHMIDT,1812)	57	50	40	51	44	52	294	49.00	45.94
Calathus metallicus DEJEAN,1828	24	17	29	21	22	15	128	21.33	20.00
Pterostichus pilosus (HOST,1789)	19	14	16	18	16	12	95	15.83	14.84
Carabus sylvestris PANZER,1796	5	7	9	5	8	4	38	6.33	5.94
Trechus striatulus (PUTZEYS,1847)	5	4	2	6	3	5	25	4.17	3.91
Cychrus attenuatus (FABRICIUS,1792)	4	2	3	1	4	5	19	3.17	2.97
Pterostichus unctulatus (DUFTSCHMIDT,1812)	1	2	2	1	3	5	14	2.33	2.19
Carabus violaceus LINNAEUS,1758	3	1	1	1		3	9	1.50	1.41
Pterostichus pumilio (DEJEAN,1828)	1	1		2		1	5	0.83	0.78
Calathus micropterus (DUFTSCHMIDT,1812)		2		1	1	1	5	0.83	0.78
Cychrus caraboides (LINNAEUS,1758)	1	1	1		1		4	0.67	0.63
Deltomerus tatricus (L. MILLER,1859)			1		1		2	0.33	0.31
Leistus piceus FROELICH,1799					1		1	0.17	0.16
Carabus linnei PANZER,1813			1				1	0.17	0.16
Number of individuals	120	101	105	107	104	103	640	106.67	
Number of species	10	11	11	10	11	10	10		

fied in subalpine meadows in and/or above the zone of disintegration of continuous dwarf pine stands. The higher humidity is able to compensate differences in structure and spatial structure of vegetation.

These apparent differences in habitat requirements, however, should be taken in consideration in interpretation of results of different studies on impacts of different human activities or natural disturbances and catastrophes in mountain ecosystems to exclude false conclusions and, as a consequence, to avoid incorrect decisions in management of landscape and nature protection.

Acknowledgements

This study was financially supported by the grant agency VEGA – project 2/2004/4086. The author also thanks to the Ministry of Environment of Slovak Republic for allowance to work in the strictly protected areas and to the Administration of State Forests of the TANAP for support during collection of the material in the field.

Literature

BURMEISTER, F., 1939: Biologie, Ökologie und Verbreitung der europäischen Käfer. Hans Goecke Verlag, Krefeld, 397 pp.

CHOMICZ, K., ŠAMAJ, F., 1974: Zrážkové pomery. p. 443–536. In: M. KONČEK (ed.): Klíma Tatier, Veda, Bratislava, 855 pp.

CRISTAND-PESKOLLER, H., JANETSCHEK, H., 1976: Zur Faunistik und Zoozönotik der südlichen Zillertaller Hochalpen. Veröffentlichungen Universitäts Innsbruck, Alpin-Biologischen Studien, 7: 1–134.

DE ZORDO, I., 1979: Ökologische Untersuchungen an Wirbelosen des zentralalpinen Hochgebirge (Obergurgel Tirol), III. Lebenscyklen und Zönotik von Coleopteren. Veröffentlichungen Universitäts Innsbruck, Alpin-Biologischen Studien, 9: 1–131.

GROSSENSCHALAU, H., 1981: Ükologische Valenz der Carabiden (Ins. Coleoptera) in hochmontanen, naturnahen Habitaten des Sauerlandes (Westfallen). Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen, 43: 3–33.

HŮRKA, K., 1996: Carabidae České a Slovenské republiky, Kabourek, Zlín, 5665 pp.

RANDUŠKA, D., VOREL, J., PLÍVA, K., 1986: Fytocenológia a lesnícka typológia. Príroda, Bratislava, 343 pp.

RAUŠER, J., ZLATNÍK, A., 1966: Biogeografie (mapa č. 21). In: Atlas ČSSR, Praha.

ŠAMAJ, F., 1978: 28 Zrážky (rok), 29 Zrážky (chladný polrok), 30 Zrážky (teplý polrok). In: E. MAZÚR (ed.) Atlas Slovenskej socialistickej republiky, Kapitola V. Ovzdušie a vodstvo. Slovenská academia vied a Slovenský úrad geogézie a kartografie, Bratislava.

ŠKVARENINA, J., TOMLAIN J., KRIŽOVÁ E., 2002: Klimatická vodní bilance vegetačních stupňů na Slovensku. Meteorologické správy, 55: 103–109.

ŠUSTEK, Z., 1984: Carabidae and Staphylinidae in two forest reservations and their reactions on surrounding human activity. Biológia (Bratislava), 39: 137–162.

ŠUSTEK, Z., 1984: Influence of clear cutting on ground beetles (Coleoptera, Carabidae) in a pine forests. Communicationes Inst. For. Čechoslov., 12: 243–254:

ŠUSTEK, Z., ŽUFFA, M., 1986: Spoločenstvá bystruškovitých a drobčíkovitých (Coleoptera, Carabidae et Staphylinidae) Štátnej prírodnej rezervácie Šrámková. Ochrana prírody, 7: 347–374.

ŠUSTEK, Z., ŽUFFA, M., 1988: Spoločenstvá bystruškovitých a drobčíkovitých (Coleoptera, Carabidae et Staphylinidae) Štátnej prírodnej rezervácie Kľačianska Magura v Chránenej krajinnej oblasti Malá Fatra. Ochrana prírody, 9: 229–251.

ŠUSTEK, Z., 2000: Spoločenstvá bystruškovitých (Coleoptera, Carabidae) a ich využitie ako doplnkovej charakteristiky geobiocenologických jednotiek: problémy a stav poznania. p. 18–30. In: ŠTYKAR, J. et ČERMÁK, P. (eds): Geobiocenologická typizace krajiny a její aplikace. Geobiocenologicke spisy, svazek č. 5. Brno, pp. 136.

ŠUSTEK, Z., 2002: Seasonal changes in distribution of ground beetles (Coleoptera, Carabidae) along a discontinuous seminatural windbreak. p. 143–148. In MADĚRA, P. (ed.): Ekologické sítě. Sborník příspěvků z mezinárodní konference 23.–24.11.2001 v Brně. Geobiocenologické spisy. sv. 6, MZLU v Brně a MZE, Praha, 2002, 273 pp.

ŠUSTEK, Z., 2004. Carabid communities (Col. Carabidae) in degradation stages of pubescent oak forests (Corni Quercta deg.) in oak vegetation tier. p. 203–209. In: POLEHLA, P. (ed.), Hodnocení stavu a vývoje lesních geobiocenóz. Geobiocenologické spisy, svazek 9. Lesnická a dřevařská fakulta MZLU v Brně, Ústav lesnické botaniky, dendrologie a typologie. Brno, 249 pp.

ŠUSTEK, Z., 2006: Cenozele Carabidelor din ecosistemele alpine şi subalpine din Carpaţi Occidentali. Oltenia, 22: 233–242.

THIELE, H. U., 1977: Carabid beetles in their environments. Springer Verlag, Berlin, Heidelberg, New York, 369 pp.

ZLATNÍK, A., 1976: Lesnická fytocenologie, Praha, 495 pp.