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Habitat selection of ground-dwelling beetles during dolomitic succession

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Abstract - Changes of habitat fidelity and habitat selection indices, based on the indices developed by BUSE (1988), were studied on beetles of different successional stages in the Buda Hills, near Budapest, Hungary. Habitat selection of beetle species ranged from habitat specialists to habitat generalists, but it did not show any trends along the successional gradient. There were differences in mean habitat fidelity among the beetles of different feeding types. In the present study, temporal changes of habitat selection depended on the overwintering strategies and the feeding claims of the species. With 3 tables and 2 figures.

INTRODUCTION

The role of habitat in the distribution of species is one of the basic problems in ecology (e.g. MACARTHUR 1972, CODY 1985). Description of the occurrence of beetle (Coleoptera) species in different habitats has a long history (FABRICIUS 1801, KUTHY 1896). THIELE (1977) reviewed the distributions of carabid species in relation to habitat. Recently studies designated to investigate the ecological relationships between habitat characteristics and beetle populations (BUSE 1988).

The aim of this study is to investigate the differences of habitat fidelity among ground-dwelling beetle species, and to study temporal changes of it in different stages of dolomitic succession in Hungary.

STUDY AREA AND METHODS

The study site is situated near Budapest in the Buda Hills (47° 35' N, 18° 90' E) in Hungary. The rock was dolomite in the study area. We selected four study sites reflecting to the most typical phases of dolomitic succession. The plant associations were ranged according to JAKUCS (1981).

I. Open dolomitic grassland *(Seseli leucospermo-Festucetum pallentis)*. The plant cover is not complete, the grass/rock ratio is about 50% - 50%.

II. Dolomitic steppe meadow *(Chrysopogono-Caricetum humilis)*. The plant cover is almost closed, the grass/rock ratio is about 95% - 5%. This area situated on the southern side of hill.

III. Closed dolomitic grassland *(Festuco pallenti-Brometum pannonici)*. The area is totally covered with vegetation, and situated on a northern slope.

IV. Sessile-turkey oak forest *(Quercetum petraeae-cerris)*. The trees are not too high (10-15 m), because of the shallow soil.

We put 108 pitfall traps in each of the habitats, altogether we had 432 traps. The mouth diameter of the jars was 9 cm. The investigation went on from April to October in 1988. Traps were sampled in every two weeks. We used for each species an independent and comparable habitat fidelity index for each habitat, developed by BUSE (1988). The formula was:

$$\text{habitat fidelity} = (pH_i - pH_i')/(pH_i + pH_i')$$

where $pH_i = n_i/n$ and $pH_i' = (n-n_i)/((N-1)*n)$, n_i: number of individuals in habitat i, n: number of individuals in all habitats, N: number of habitats, H_i: habitat i, H_i': all habitats except i.

The values of this index ranged from -1 to +1. The maximum value, +1 showed that all individuals of the given species were in the given habitat, whereas -1 indicated that no individuals of the species were recorded in the habitat, and 0 indicated that there was an average number of individuals in the habitat (BUSE 1988). The sum of absolute values of the four indices for a species gives the habitat selection index of the species (BUSE 1988).

To avoid increasing noise in abundance of less dominant species, the 22 most abundant species out of the total 349 were selected for the analyses of habitat selection and habitat fidelity. In this data set more than 100 individuals were presented for all of the habitats. The records of the fourteen trap controls were pooled.

The beetle species were clustered into five groups based on their feeding types. These five groups were the following: herbivores, predators, scavengers, dung feeders and detritus feeders.

For agglomerative cluster analysis the statistical program package of SPSS\PC+ (NORUSIS 1986) was applied, choosing the squared Euclidean distance measure. The same program package was applied for correlation analysis.

For the analysis of temporal changes of habitat fidelity and habitat selection the six most abundant beetle species were selected. Traps which collected less than ten individuals of a species during the two week period were omitted from the analysis of temporal changes.

Table 1. Values of habitat fidelity and habitat selection indices for beetle species of different stages of dolomitic succession. The species were grouped into five groups according to their feeding types (A - predators, B - dung feeders, C - scavengers, D - detritus feeders, E - herbivors)

	Habitat fidelity index				Habitat Selection Index HSI	Mean HSI
	Oak forest	Dolomitic steppe meadow	Dolomitic grassland			
			Open	Close		
A. Pseudocypus picipennis	-0.60	0.29	-0.83	0.52	2.25	
Carabus convexus	0.97	-0.98	-0.95	-0.95	3.85	
Calathus fuscipes	-0.48	0.84	-1.00	-1.00	3.31	
Pterostichus melas	0.99	-0.97	-0.99	-1.00	3.96	3.21
Abax ater	1.00	-1.00	-1.00	-1.00	4.00	
Ocypus olens	0.40	-0.49	-0.86	-0.12	1.87	
B. Onthophagus fracticornis	-0.58	0.87	-0.98	-1.00	3.43	
Geotrupes vernalis	0.77	-0.39	-0.89	-0.99	3.04	
Sisyphus schaefferi	-0.50	0.71	-0.59	-1.00	2.81	3.07
Onthoph. grossepunctatus	-0.35	0.67	-0.69	-1.00	2.71	
Onthophagus nutans	0.84	-0.50	-1.00	-1.00	3.34	
C. Thanatophilus rugosus	0.00	0.56	-0.91	-0.98	2.46	
Nicrophorus humator	0.62	-0.51	-0.42	-0.97	2.53	2.40
Nicrophorus vespillo	0.68	-0.43	-0.60	-1.00	2.71	
Nicrophorus vespilloides	0.38	-0.05	-0.45	-1.00	1.88	
D. Pedinus femoralis	-1.00	-0.02	0.61	-0.99	2.63	
Gnaptor spinimanus	-0.98	0.00	-1.00	0.59	2.58	3.14
Crypticus quisquilius	-1.00	0.85	-0.84	-0.65	3.35	
Amphotis marginata	-1.00	-0.98	-1.00	1.00	3.98	
E. Zabrus spinipes	-1.00	-0.29	-1.00	0.76	3.04	
Cetonia aurata	-0.92	-0.78	-0.85	0.87	3.42	3.44
Potosia cuprea obscura	-1.00	-0.89	-0.98	0.97	3.84	

RESULTS

23181 individuals were registered in all of the habitats belonging to the selected species for analysis (see above). Values of habitat fidelity and habitat selection indices are shown in Table 1.

There were only two cases when a species occurred in only one habitat, but there were twenty one cases, when a beetle species avoided a habitat. The values of the habitat selection index ranged from 0 to 4. The average value of this index for the 22 abundant species is 3.05, which indicates a strong habitat selection.

The 22 most abundant beetle species were clustered into four groups by cluster analysis (Fig. 1), based on their habitat fidelity values. Group I, II, III and IV consists of species which preferred forest, dolomitic steppe meadow, open dolomitic grassland, and closed dolomitic grassland habitats, respectively.

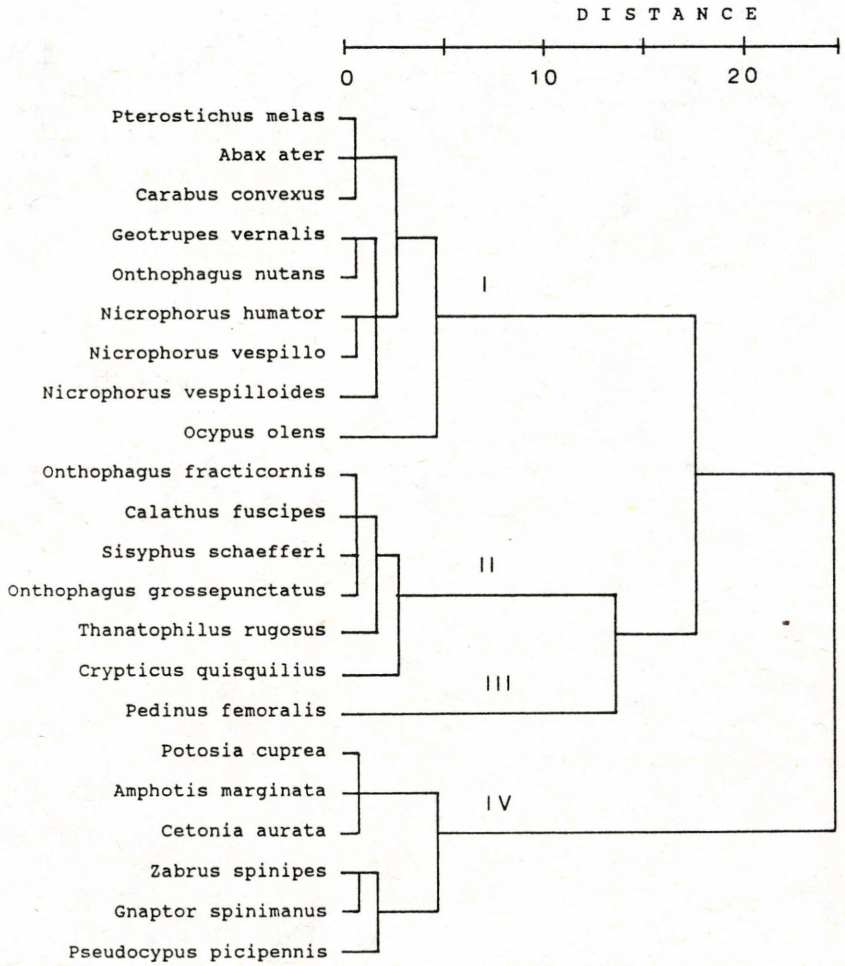

Fig. 1. Dendogram of cluster analyses of beetle species, based on habitat fidelity indices. Number I, II, III and IV refer to forest, dolomitic steppe meadow, open dolomitic grassland and closed dolomitic grassland habitats, respectively.

Table 2. Values of mean habitat fidelity and habitat selection indices of the four beetle species groups, separated by cluster analysis. See text and Fig. 1 for explanation of symbols I, II, III and IV.

	Oak Forest	Dolomitic steppe meadow	Open dolomitic grassland	Closed dolomitic grassland	Habitat selection index
I (n=9)	+0.74	-0.59	-0.79	-0.89	3.02
II (n=6)	-0.49	+0.75	-0.84	-0.94	3.02
III (n=1)	-1.00	0.00	0.61	-0.99	2.63
IV (n=6)	-0.92	-0.44	-0.94	0.79	3.09

According to the mean values of habitat fidelity and habitat selection indices, the forest and the dolomitic steppe meadow habitats seemed to be similar, but these indices showed higher values in the case of the closed dolomitic grassland (Table 2). It means that the closed dolomitic grassland is less similar to the other habitats. Where the habitats were bordering, the error of the habitat selection caused by random movement of individuals increased, like in the case of the forest and the dolomitic steppe meadow habitats. Only one species was found in the open dolomitic grassland (*Pedinus femoralis*), therefore we did not use this habitat for comparison.

There was not any significant difference between the mean habitat selection index of generalists (scavengers, dung feeders and detritus feeders) and that of specialists (herbivores and predators) (two-tailed t-test; d.f. = 20, t = 1.39, n.s.).

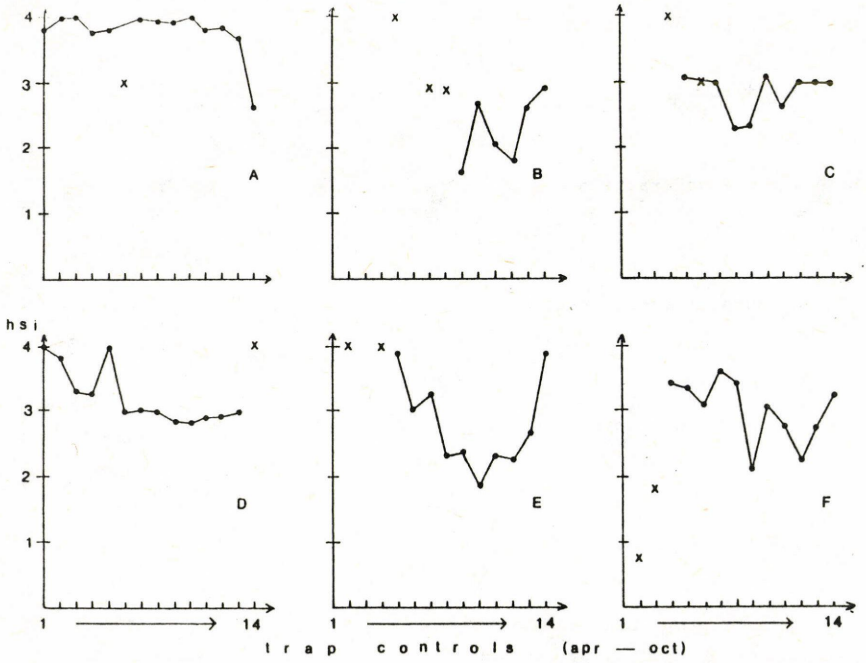

Fig. 2. Changes of habitat selection indices of the six most abundant beetle species, from April to October. The x refer to trap recordings, where less than ten individuals were caught (see text). (hsi = habitat selection index). - A = *Carabus convexus*, B = *Nicrophorus vespilloides*, C = *Nicrophorus vespillo*, D = *Pedinus femoralis*, E = *Sisyphus schaefferi*, F = *Geotrupes vernalis*

The number of individuals of the 6 beetle species used in the temporal analysis showed great oscillation, but the values of the habitat selection index did not correlate with the number of individuals, therefore the different number of individuals did not affect the results.

The values of the habitat selection index usually decreased during the study period (Fig. 2), but this decline proved to be significant only in the case of *Carabus convexus* and *Pedinus femoralis* (Table 3). Habitat selection of the two *Nicrophorus* species *(N. vespillo, N. vespilloides)* showed great oscillations without any trends. In the case of *Sisyphus schaefferi* and *Geotrupes vernalis* the habitat selection showed certain trends, without any significance.

The number of individuals did not correlate significantly with time, therefore the error caused by the great variance of numbers did not influence the results.

DISCUSSION

During ecological succession there are significant changes in the composition and structure of vegetation (e.g. RICKLEFS 1976, MACMAHON 1980, TILMAN 1985). Beetle communities show strong relationships with the structure of vegetation during succession (BROWN & HYMAN 1986, HENDRIX et al. 1988, BÁLDI 1990, WALICZKY in press). Habitat fidelity index of species help to reveal these relationships in details, measuring the tolerance of species for a suboptimal or optimal habitat.

Table 3. Correlation values between the habitat selection indices, number of individuals and time in the case of the six most abundant beetle species. (Pearson's correlation coefficient, number of valid trap records, one-tailed significance.)

	Correlation between:		
	Habitat selection index and Number of individuals	Habitat selection index and Time	Time and Number of individuals
Carabus convexus	0.274 13 0.182	-0.523 13 0.033	-0.109 13 0.362
Geotrupes vernalis	0.171 11 0.307	-0.497 11 0.060	0.345 11 0.149
Pedinus femoralis	-0.245 13 0.210	-0.781 13 0.001	-0.48 13 0.438
Sisyphus schaefferi	0.493 10 0.074	-0.215 10 0.275	-0.482 10 0.079
Nicrophorus vespillo	-0.281 9 0.232	0.188 9 0.314	-0.463 9 0.105
N. vespilloides	-0.501 6 0.156	0.596 6 0.106	-0.163 6 0.379

There are habitat specialists and habitat generalists among beetle species (WITOWSKI 1978), and generalists can be found in more types of habitats than specialists (HANSKI 1982a, 1982b). In the present study values of the habitat selection index ranged from 1.87 to 4.00, supporting this statement. At the individual level the habitat preference may be distinct or shared (ROSENZWEIG 1985). The predator species *Ocypus olens* distinct in the close dolomitic grassland habitat. In the forest three other predator species, namely *Carabus convexus*, *Pterostichus melas* and *Abax ater* shared the habitat, therefore they showed similarly high habitat preference.

At the group level the herbivores were the most habitat specialists. According to BUSE (1988) this is the result of the requirements of a beetle species for a specific host plant species.

Some of the congeneric species showed different habitat preference. For example *Pseudocypus picipennis* occurred in the close dolomitic grassland, but *Ocypus olens* preferred the oak forest. Two *Onthophagus* species *(O. fracticornis* and *grossepunctatus)* preferred the dolomitic steppe meadow, but the third species *(O. nutans)* preferred the forest. Three *Nicrophorus* species *(N. humator, N. vespillo, N. vespilloides)* showed another type of habitat preference, each of them preferred the forest habitat.

The mean habitat fidelity values, ranked into successional order, showed high values in the close dolomitic grassland, and lower values both in the dolomitic steppe meadow and in the oak forest. The open dolomitic grassland habitat was not considered here, because it had only one characteristic species, namely *Pedinus femoralis*.

Temporal changes of the habitat selection index did not correlate with the number of individuals. The habitat selection index of *Carabus convexus* and *Pedinus femoralis* significantly decreased with time, because humidity decreased and food became less abundant in summer, therefore the individuals dispersed to search better conditions. The habitat selection index of the *Sisyphus schaefferi* showed a similar pattern to the changes of the previous species in the first half of the study, but the values of the index increased in the second. The difference may be the consequence of different overwintering strategies of the species. *Carabus convexus* and *Pedinus femoralis* overwinter as a larva, but *Sisyphus schaefferi* mostly as an imago. The two *Nicrophorus* species are generalists (see below), therefore they had not significant claims for a specific habitat. The values of habitat selection index of *Geotrupes vernalis* showed large oscillations, therefore the temporal changes were not significant, though the habitat selection of the species seemed to be decreased.

Among the five feeding types which we separated (Table 1), the herbivores and somewhat the predators may be considered as specialists, because of their claims for specific food. The dung feeders, detritus feeders and scavengers are rather considered as generalists. The values of habitat selection index supported this hypothesis, because the herbivores and predators had higher habitat selection values than the others. The scavengers showed the lowest value of habitat selection index. This may be due to their attraction to the traps from large distances because of the smell of dead beetles.

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