

**Studies on carabid assemblages and life-history characteristics of two
Carabus (Coleoptera, Carabidae) species**

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Contents

Contents.....	2
1 Overview and main objectives	3
2 Section I. – Spatio-temporal fluctuations of carabid assemblages in forested habitats	6
2.1 Introduction	6
2.2 Materials and methods	11
2.2.1 Study area and sampling	11
2.2.2 Methods of analyses	12
2.3 Results.....	16
2.3.1 Assemblage characteristics.....	16
2.3.2 Diversity profiles.....	20
2.3.3 Overall species composition.....	22
2.3.4 Investigation of characteristic species.....	23
2.3.5 Body-size categories and habitat affinity categories by habitat types and years	25
2.3.6 Species-specific responses	28
2.4 Discussion	34
3 Section II. - Life-history characteristics of two <i>Carabus</i> species.....	39
3.1 Introduction	39
3.2 Materials and methods	45
3.2.1 Study species	45
3.2.2 Study area and sampling	51
3.2.3 Age determination	52
3.2.4 Data analysis	54
3.2.5 Species-habitat modelling	55
3.2.6 ‘Seasonality models’	55
3.3 Results.....	56
3.3.1 General results	56
3.3.2 Age composition based on mandible wear	61
3.3.3 Reproductive characteristics of females based on the examination of ovaries ..	67
3.3.4 Number of ripe eggs found in the ovaries	70
3.3.5 Species - habitat and seasonality modelling	70
3.4 Discussion	73
3.4.1 <i>Carabus scheidleri</i>	73
3.4.2 <i>Carabus ullrichi</i>	75
4 Overall conclusion	78
5 References	81
6 Acknowledgements.....	92
7 Summary	94
8 Összefoglaló.....	96

1 Overview and main objectives

One of the cornerstones of conservation planning is the identification of priority areas for biodiversity conservation (Margules & Pressey 2000). Many studies have focused on various species indicator groups in identifying area networks for the conservation of biodiversity. Besides, some studies have tested successfully the usage of species attributes of different indicator groups (Baguette & Schtickzelle 2006; Cleary et al. 2009). Ground beetles are among these good ecological indicators, because their taxonomy and ecology are well documented (Lövei & Sunderland 1996) and many studies proved their sensitiveness to habitat alterations/disturbance. The ground beetles (Carabidae) is a speciose family of Coleoptera, containing more than 40 000 described species classified into some 86 tribes (Erwin 1985). They constitute a significant portion of the fauna active on the ground surface at most of their area of occurrence, and are among the best known insect taxa in the Northern Hemisphere (Lövei & Sunderland 1996). The abundance, species richness and attractive coloration of many species have made carabids popular objects of studies for entomologists (Lövei & Sunderland 1996). According to Lövei (2008) carabids might have been used as indicator organisms for a) assessments of environmental pollution (Heliovaara & Vaisanen 1993), b) habitat classification for nature protection (Luff et al. 1992, Luff 1996; Pizzolotto 1994), c) characterization of soil-nutrient status in forestry (Szyszko 1983) and, d) they might also be biodiversity indicators (Niemelä et al. 2000). Furthermore, carabids are relatively long-lived animals allowing sampling to be carried out by easy-to-use pitfall traps (Lindroth 1974). All of these issues make carabids suitable organisms for assessing microhabitat selection or seasonality on small spatio-temporal scales. The seasonality could provide a snapshot about the viability of the population; some quantitative description methods are now available (Fazekas et al. 1992; Pokluda et al. 2011; Bérces & Elek 2012). Moreover environmental change-related concerns make it relevant to have a more precise understanding of the spatial and temporal variation in the seasonal dynamics of ground beetles. Given that several species are protected, such information would be useful to harmonise conservation efforts during habitat management operations, like the use of chemicals in agricultural lands, forest management, etc., to minimise risk to non-target ground beetles. Throughout their worldwide distribution and abundance, ground beetles also prove a reliable snapshot about the conservation status of the studied habitat types.

This thesis is divided into two major sections. Both sections consist of the relevant introductory part, describe the designs of the investigations and then the main results of the studies are presented; afterwards these results are discussed in the context of conservation of ground beetles.

Based on long term investigations within the framework of the Man and the Biosphere Programme (MAB) the first section of this thesis contains relevant information on habitat fragmentation and forest management throughout the fluctuations of carabid assemblages. One of the purposes of this study was to describe and assess the possible role of small-scale spatial heterogeneity occurring in forest ecosystems on the composition of ground beetle assemblages in the Pilis Biosphere Reserve, in Hungary, in the course of a long-term investigation, covering the period of twenty years (1986-2006). Long-term studies describing year-to-year variability in the catch of carabid species are rare, and some of the longer studies do not show the number of individuals caught per year and location separately (Günther & Assmann 2004). In the present long-term investigation, we also examined the temporal variation of the abundance and species richness of carabid assemblages inhabiting this MAB reference site, recovering from a forest-management period.

The main aim of our research was to study the distribution of carabid assemblages between two small forest fragments (circa 0.5 ha) and the adjacent transition zone within these in the Simon Valley of Pilis Mountains, Northern Hungary. We tried to provide appropriate answers for the following questions:

1. Are carabids able to reflect changes in traits of habitat at small spatial scale (within 100 meter) among habitats?
2. Is there any difference between the studied habitat types (beech, oak and transition zone) based on the abundance and species richness of ground beetles?
3. How do the composition and abundance of the carabid assemblages change in time in the studied habitat?

The second part of this thesis includes information on the life-history characteristics of two *Carabus* species containing data on their seasonal activities, age composition and reproductive characteristics and also reviews current knowledge of life-history characteristics of ground beetles and the effects of habitat fragmentation on carabids. We tested the two studied species in the fields, and we tried to provide answers to some fundamental questions such as: At what age should the species mature? How many offspring should a female have

(ripe eggs found in the ovaries of the females)? Should they reproduce once or more? And how long should they live? Through addressing these questions life-history theory has made a major impact on our understanding of adaptation by natural selection, the most fundamental issue in all of evolutionary biology (Fabian & Flatt 2012). Another aim of this study was to examine the usefulness of two different age-estimating methods (based on the mandible wear and the development stages of the ovaries), and to investigate the habitat preference and the components of the reproductive strategies of two *Carabus* species. Our objective was to describe the patterns of seasonal activity, age structure, and reproductive characteristics, such as different ovarian stages, number of ripe eggs of a *Carabus scheidleri* population living in an abandoned agricultural field in Hungary. We also intended to present the classification of this species into one of the breeding categories already discussed in the literature. The second study species was *Carabus ullrichi* captured in woodland habitats in Hungary, already mentioned above (Pilis Biosphere Reserve). Besides the examination of seasonality, age-composition and reproductive characteristics of this large carabid species, we also assessed the habitat selection of this species considering the effects of environment conditions that might influence the distribution of *C. ullrichi*. We examined whether there were any differences in the abundance and seasonal activity patterns among three different habitat types (beech, oak and transition zone).

In summary, our main questions were the followings:

1. How does the seasonal activity pattern of the two *Carabus* species' populations change during and between years?
2. How does the age-structure of the two *Carabus* species' populations change during and between years?
3. What are the differences between the reproductive characteristics and the life-cycles of the two *Carabus* species?
4. In which cases can the two different age-estimating methods be applied together or independently?

2 Section I. – Spatio-temporal fluctuations of carabid assemblages in forested habitats

2.1 Introduction

The appearance of 'biodiversity' as a fundamental issue in conservation reflects the realization that spatial and temporal variation is essential for the continuing functioning of ecological systems (Wilson 1992; Haila et al. 1994). Thus, recording mere 'change' is a starting point when evaluating ecological consequences of human activities. What matters is the relationship between human-induced change and change occurring naturally (Haila & Levins 1992); the question is whether human activities modify the dynamics of natural change?

A major complication is addressing the question whether ecological processes operating at different scales also cause different kinds of 'change' simultaneously (Levin 1992). These different scales should be considered simultaneously, but processes at each level should be maintained distinct from each other (Haila et al. 1994). Defining adequate scales is primarily an empirical problem and depends on the ecological processes in which one is interested (Wiens 1989). An important distinction in ecological scaling is between individual-scale and population scale processes (Wiens 1989). For instance, for recording local extinctions, observations must be made on the scale of local populations (Haila et al. 1994).

This issue is well-known even in the forest ecology where several studies proved that the forest management is about simplifying tree species composition, homogenising tree age structure, and fragmenting forested landscapes (Niemelä et al. 2007). As a consequence, managed forests are relatively young overall, usually consist of smaller fragments with more edge habitats, and are exposed to novel disturbance regimes. Habitat loss is often included into the concept of habitat fragmentation, and it is usually difficult to separate the effects of habitat loss from that of fragmentation *per se* on the biota (Saunders et al. 1991).

It is also known that many species are negatively affected by the habitat fragmentation (McGeoch 1998; Niemelä 2001). The assessment of the habitat fragmentation on well-known taxa may provide important information for conservation efforts. The ground beetles are

indicator taxa according to their abundance and species richness. These are appropriate organisms for ecological assessments, such as monitoring habitat fragmentation (Lövei & Sunderland 1996; Luff 1996). Forest fragmentation affects carabid assemblages in several ways (Niemelä 2001) such as impoverishment of the assemblages especially the loss of forest specialist species. Species richness used as a measure of conservation value may be misleading, because disturbances may favour widespread and abundant generalists, leading to increased species richness as in the case for carabids (Niemelä 1996). In some cases it might occur that the forest fragmentation and the size of a fragment appear not to be crucial for the survival of the majority of forest carabids, as they tend to be distributed over various successional stages (Davies & Margules 1998). However, sensitive species requiring certain structural elements of old-growth forests, such as abundant large-sized dead wood, lush patches of mesic vegetation or wet spruce mires, or microclimatic conditions created by closed canopy, suffer from forest fragmentation. In general, species richness and the abundances of generalists and open-habitat species increased following forest cutting (Haila et al. 1994; Halme & Niemelä 1993), meanwhile those of forest-associated species decreased, which may lead to the loss of the major elements of forest biodiversity in insects. However, such species may occur in recently clear-cut sites for a few years (Koivula 2002). There are three types of carabid beetle responses to forestry practices. In strongly managed stands, such as clear-cuts: 1) Individuals of forest species caught in the clear-cut may be colonizers from nearby mature stands (Spence et al. 1996). 2) Catches of forest species may represent populations on their way to local extinctions (or drastic decrease). Since some carabids may live for at least 2-3 years, these species can persist for some time in the clear-cuts. 3) Some species with more generalist life style may be able to tolerate natural disturbances better and may survive in clear-cut sites. A drastic change usually occurs at canopy closure that takes place in a boreal region ca. 20-30 years after clear-cutting (Koivula et al. 2002). Interestingly, the closed canopy boreal forest appears to be a rather hostile environment for many carabid species, as only a few species are able to thrive (Koivula et al. 2002), resulting a peculiar species-abundance distributions in which there is a gap between the dominant species and the scarce ones (Niemelä 1993). From a conservation point of view, species requiring mature closed-canopy forest are of concern. Their habitat continues to become fragmented and lost (Niemelä et al. 2007). In the temperate zone there are fewer results regarding carabids' survival, concerning the changes in the compositions of the carabid assemblages after forest practices, within the recovering of managed forest habitats.

Forest management abandonment may benefit specialist species with contrasted ecological requirements: forest specialist and open land species (Toïgo et al. 2013). The richness of forest-dwelling, wingless and carnivorous species was mostly affected by specific habitat features and especially increased by basal area index (the sum of the cross sections taken at breast height of the trees – m²/ha) and active humus forms. Consequently, the most forest-specific and dispersal-limited component of carabids (i.e. forest-specialists and wingless species) require either unmanaged or mature stands with a closed canopy. In terms of conservation, such stands may therefore play an important role both in managed and unmanaged forests. It cannot be excluded that a more intensive silviculture which reduces total basal area might erode forest carabid biodiversity. Nevertheless, the relatively low magnitude of these results might be attributed either to the rather extensive style of forest management in their study sites (thinning, selective cutting) or to the relatively recent abandonment of forest management in the reserves (15–45 years) (i.e., Toïgo et al. 2013)

In the light of the carabids' ecology in the Northern hemisphere Niemelä (2001) suggests that the habitat specialist species are among the most threatened ones. This is especially true to for the large bodied forest carabids, which have declined more than the smaller ones because of their lower reproductive output and lower dispersal power (Koivula et al. 2002). Therefore, as forest carabids are among the threatened species, it is important to improve the conservation of the natural forest remnants.

There is a few available information on the temporal variation of the ground beetles' population dynamics (e.g., Desender et al. 2007; Scott & Anderson 2003). According to Desender et al. (2007) there are few instances of long-term studies of carabids, apart from succession studies. The six or more years' data currently available for long-term monitoring sites in the United Kingdom form a valuable source of information on annual fluctuations of abundance data which, in the longer term, will greatly enhance understanding of the response of carabid communities to change (Scott & Anderson 2003). In conclusion, we would agree with Eyre et al. (1996) that “there is great potential for the use of ground beetle data from structured, standardised surveys in assessing environmental quality” and would add that their potential as indicators of the effects of environmental change appears just as great.

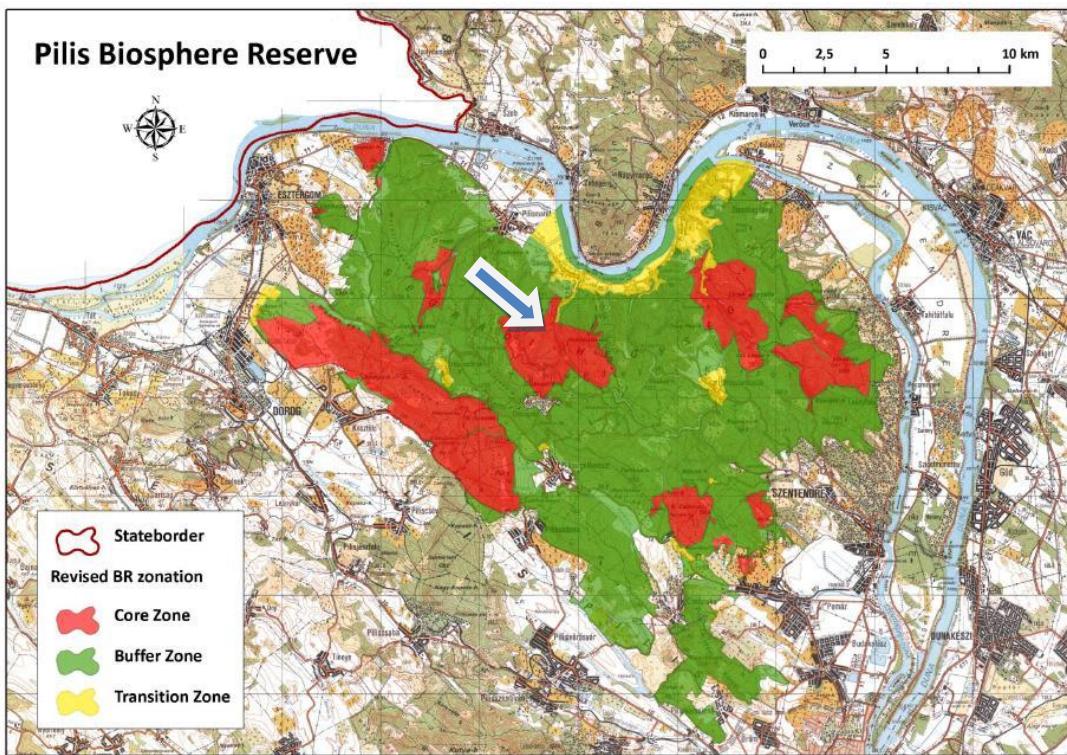
In the conservation policy of European countries, there is a long tradition to identify and to assign areas for long-term monitoring. The Man and the Biosphere Programme (MAB)

proposed an interdisciplinary research agenda and capacity building aiming at improving the relationship of people with their environment globally. Launched in the early 1970s, it notably targets the ecological, social and economic dimensions of biodiversity loss and the reduction of this loss. It uses its World Network of Biosphere Reserves as a possible vehicle for knowledge-sharing, research and monitoring, education and training, and participatory decision-making (<http://www.unesco.org>). Concerning on the conservation/ecological approaches, there are two action plans within the MAB programme:

Action 1.) Contribute to minimizing biodiversity loss through the use of ecological and biodiversity sciences in policy- and decision-making;

Action 2.) Promote environmental sustainability through the World Network of Biosphere Reserves.

In 1982, the MAB project was started in the Pilis Biosphere Reserve (PBR) (Map 1), a woodland region in Hungary. PBR is situated to the north of Budapest, bordered by the Danube River to the north and east, and by the Vörösvár Valley in the southwest. Geologically, the territory comprises two parts: the Eastern and Southern areas are part of the sedimentary rocks of the Pilis Mountains. The rest belongs to the volcanic ranges of the Szentendre-Visegrád Mountains. Dense oak and beech forests almost completely cover the area. These forest ecosystems are unmanaged since 1982, which means that no regular forestry service were used in these habitats, and are devoted to tourism and recreational purposes (<http://www.unesco.org>).



Map 1. Pilis Biosphere Reserve (source: www.termeszetvedelem.hu). PBR = Pilis Biosphere Reserve

Judgement of the conservation needs of Carabidae is often focused upon specific habitat types (Eyre et al. 2001), geographically restricted areas (Kubach et al. 1999), even individual localities (Magura et al. 2000) or individual species (Assmann & Jansen 1999). Carabid beetles are among the best studies taxa regarding the effects of forest management, even in the boreal region (Niemelä et al. 2007). Forestry practices often result in the fragmentation of the original forest landscape. Long-term studies describing year-to-year variability in the catch of carabid species are rare, and some of the longer studies do not show the number of individuals caught per year and location separately (Günther & Assmann 2004). In this current approach, we examined the spatio-temporal variation of the abundance and species richness of carabid assemblages inhabiting this MAB reference site by a long-term investigation. Before 1982 forest management practices were regularly applied, such as thinning. Between the period of 1982 and 1984 the target area was occasionally treated. Thus, we examined carabids inhabiting in the target area after the abandonment of forest-management.

2.2 Materials and methods

2.2.1 Study area and sampling

The study area was located in the Pilis Biosphere Reserve, in the Pilis Mountains, 50 km from Budapest towards North (GPS coordinates: N 47°45'06.39", E 18°54'38.94", mean altitude 267 m). As already mentioned above, prior to 1982 forest management practices were regularly applied, such as thinning (Kádár *pers. comm.*). Between the period of 1982 and 1984 the target area was occasionally treated, which means that an irregularly used forest road was created between the two studied forested habitats (Kádár *pers. comm.*). Since 1982 no regular forestry treatments were applied and the area was devoted to tourism and recreational purposes (<http://www.unesco.org>). The forest stands were similar in their size, circa 0.5 ha of each was used for sampling.

Three forested habitats were sampled during the study (Picture 1):

- (1) Beech forest (*Melittio-Fagetum*) where the dominant tree species were the beech (*Fagus sylvatica*), and the hornbeam (*Carpinus betulus*) in the canopy, but the sycamore (*Acer pseudoplatanus*) was also present. In the sparse shrub layer, the gooseberry (*Ribes uva-crispa*) and mezereon (*Daphne mezereum*) were present. The herb layer was seasonally dense with wind flower (*Anemone nemorosa*), hollowroot (*Corydalis cava*) and western touch-me-not (*Impatiens noli-tangere*).
- (2) A transition zone (neighbouring the irregularly used forest road) intersected the beech forest from the adjacent oak forest. This zone was about 30 m wide dominated by *Asarum europaeum*, *Urtica dioica*, *Fragaria vesca* and nitrophilous weeds, and bordered by the beech forest on one side and by the oak forest on the other. The canopy layer was moderately closed provided by the marginal trees from the adjacent forest patches.
- (3) An oak forest (*Querco petrae-Carpinetum*) was also sampled. In the canopy, the sessile oak (*Quercus petrea*) and the hornbeam were present. The shrub layer was entirely missing, while the herb layer was dominated by the seasonally dense plants: hollowroot and buttercup anemone (*Anemone ranunculoides*).

Carabids were collected by pitfall traps (plastic cups of 80 mm diameter, 300 ml volume, containing 4% formaldehyde as a killing and preserving agent, and having a metal top above

each trap). The traps were emptied weekly from the end of April to the beginning of September always in two consecutive years, in 1985-1986, in 1993-1994 and in 2005-2006, covering a twenty-year period. Five pitfall traps were installed in each habitat, the inter-trap distance was five meters, and the traps were arranged in a row. In order to sample the core habitats we maintained a distance from the edge to at least 15 meters, both in the beech and oak forest.



Picture 1. Study area in the Pilis Biosphere Reserve. From left to right: Beech forest; Transition zone; Oak forest (Photos: Z. Elek)

The sampling was carried out by Ferenc Kádár in the first two periods (1985-86 and 1993-94) of the study. The carabid beetles from the collected material were identified based on keys of Hűrka (1996) and Csiki (1908). Identification and body size measurements of the captured individuals were done by the same person (R. Andorkó).

2.2.2 Methods of analyses

Activity density and species richness

We applied the “activity density” term for the pitfall trap catches. It refers to the abundance of that portion of a carabid population which is actively moving around and can be trapped. The term “activity density” describes the relativeness of pitfall trap catches (Southwood & Henderson 2000). The average activity density, the mean number of species per traps and the

ecological groups between the different habitat types were compared by Kruskal-Wallis and subsequently by Mann-Whitney U tests (Sokal & Rohlf 1981). The Statistica program was used for statistical calculations (StatSoft 2000).

Analyses of diversity patterns

Species diversities of the pooled samples for two-year period (to reduce the effects of abundance fluctuations (i.e. singletons, and zero counts) on the estimations of diversity profiles) of each habitat type were compared by the Rényi one-parametric diversity index family. In the case of diversity index families not just one numerical value is used to characterize the diversity of an assemblage, but a family of diversity values (Tóthmérész 1995). The one-parametric diversity indices may be portrayed graphically by plotting diversities against a scale parameter. Members of a one-parametric diversity index family have varying sensitivities to the rare and abundant species as the scale parameter changes (Lövei 2005; Tóthmérész 1998).

The Rényi diversity is a typical member of the generalized entropy functions (Ricotta 2005). It includes, as a special case, the number of species, Shannon diversity, Simpson or quadratic diversity and the dominance index (Tóthmérész 1998). When the value of the scale parameter is zero, the Rényi diversity is extremely sensitive to the contribution of the rare species to the diversity of the assemblage. When the value of the scale parameter approaches 1, then the Rényi diversity is identical to the Shannon diversity, and it is sensitive to the rare species, although less so than at 0. When the value of the scale parameter is 2, the Rényi diversity is related to the quadratic (Simpson) diversity. In this case the index starts to be more sensitive to the frequent species than to the rare ones. When the value of the scale parameter is large (approaches positive infinity), the Rényi diversity is related to the Berger-Parker dominance index that is determined only by the relative abundance of the most common species. The analyses were carried out in R 2.8.1 (R development core team 2008) using package “vegan”.

Comparison of species composition by years

In order to evaluate the differences in the species composition between the years, we applied Mantel test; when the correlation coefficient exceed 0.6, we considered the significant differences as true differences between the studied years. First we calculated the dissimilarity matrix for the dataset from every year based on the Bray-Curtis dissimilarity index (Clarke

1993). The pairwise comparisons of these matrices were done by Mantel test with 10,000 permutations (Légonde & Légonde 1998). The analyses were carried out in R 2.8.1 (R development core team 2008) using package “vegan”.

Investigation of characteristic species

The characteristic species of the habitats were explored by the IndVal (Indicator Value) procedure (Dufrêne & Légonde 1997). It is a neat and simple method to find indicator species or species assemblages characterising groups of samples or both. The novelty of this approach lies in the way that this method combines a species’ relative abundance with its relative frequency of occurrence in the various groups of samples. The statistical significance of the species indicator values is evaluated using a randomisation procedure. Indicator species are defined as the most characteristic species of each group, found mostly in a single group and present in the majority of sites belonging to that group. This duality, which is of ecological interest, is seldom completely exploited; often only the distribution of abundances in the groups is used. In these cases, species occupying only one or two sites in one habitat group and present only in that group (rare species) receive the same indicator value as species occupying all sites of that habitat group and found only in that group. However, there is an important difference between these two types of species. The first one is an asymmetrical indicator, according to the IndVal terminology: its presence cannot be predicted in all sites of one habitat, but contributes to habitat specificity. The second type of species is a true, symmetrical indicator: its presence contributes to habitat specificity and its presence can be predicted in all sites of the group. With the IndVal procedure it is possible to distinguish the two types of indicator species; species that have an indicator value $> 55\%$ are regarded as symmetrical indicator species. In many respects the IndVal approach is a quantitative characterisation of the idea of indicator species of the classical plant sociology, based on computerised randomisation procedure. The relationship of the studied habitat types (given in the typology file for IndVal) were described by hierarchical cluster analysis with group of average fusion algorithm with Bray-Curtis similarity.

Body-size categories and habitat affinity categories by habitat types and years

For numerical analyses, beetles were classified according to their body size and habitat preference. In order to classify body size, ranges from Lindroth (1985; 1986) and from Hůrka

(1996) were used to calculate geometric means, and three classes (small: 3.5–9.5 mm, medium: 9.6 – 15.2 mm and large: >15.2 mm) were established using a size distribution graph. Habitat preference classes were delineated as forest specialists, open habitat species and generalists, based on information in Lindroth (1985; 1986) and in Hürka (1996).

Species-habitat modelling

We used the following general analytical approach (based on Franklin et al. 2000) in order to study the main effects on habitat selection of carabid communities. We formed *a priori* verbal hypotheses. Our research questions were converted to statistical hypothesis, which we then expressed as models that could be fit to the available data. In these models, the response variable was species abundance per habitat type. The explanatory variable was the habitat type as fixed effect.

Based on the number of individuals caught, the modelling determines the direction of abundance change of a species over a time period and in a habitat type. The slope of the change refers to the increase or decrease of population size in time. Subsequently, by an appropriate significance measure, the slopes are compared among habitats.

During the species modelling we used generalised linear models to explore the impacts of the habitat type on the distribution of carabids. We used a count dataset (abundance data per species) for modelling. Species occurring at least 10 individuals/habitat were included in this analysis. Before the modelling, the possible dependencies among the (potential) variables were checked using Spearman rank correlation or non-parametric Kruskal-Wallis analysis of variance. We used the following variable in the model evaluation: habitat-type (beech, transition zone, oak).

2.3 Results

2.3.1 Assemblage characteristics

A total of 13 844 individuals belonging to 43 species were sampled in the studied years (Tables 1 and 2). The number of the species did not change remarkably during the years, except in the transition zone, where the number of species increased by the year 2006. However, the number of individuals showed considerable increase during the studied years, except for 1994.

We divided the species into categories according to their occurrences and activity densities among the years.

1. *species with constant occurrence and constant abundance*: We found constant species that occurred during all years of sampling, but did not show remarkable differences in the number of individuals among the years, like *Abax parallelus* (Duftschmid, 1812), *Carabus coriaceus* Linnaeus, 1758, *Harpalus atratus* Latreille, 1804, *Harpalus rufipes* (De Geer, 1774), *Harpalus marginellus* Dejean, 1828, *Notiophilus rufipes* Curtis, 1829 and *Stomis pumicatus* (Panzer, 1796).

2. *species with constant occurrence and increasing abundance during the years*. We collected species that were trapped in all studied years, and their number of individuals increased considerably during the years, like *Abax parallelepipedus* (Piller et Mitterpacher, 1783), *Abax carinatus* (Duftschmid, 1812), *Abax ovalis* (Duftschmid, 1812), *Aptinus bombarda* (Illinger, 1800), *Carabus convexus* Fabricius, 1775, *Carabus nemoralis* O. F. Müller, 1764, *Carabus ullrichi* Germar, 1824, *Molops piceus* (Panzer, 1793), *Nebria brevicollis* (Fabricius, 1792), *Platynus assimilis* (Paykull, 1790), *Pterostichus melas* (Creutzer, 1799), *Pterostichus oblongopunctatus* (Fabricius, 1787), *Pterostichus ovoideus* (Sturm, 1824) and *Pterostichus melanarius* (Illinger, 1789).

3. *species with constant occurrence and decreasing abundance during the years*. Although 78 individuals of *Trechus pilisensis* Csiki, 1918 was caught in 1985 and 1986, in 2006 we found only 15 individuals in all areas. The number of *Pterostichus niger* (Schaller, 1783) and

Leistus rufomarginatus (Duftschmid, 1812) beetles also decreased remarkably during the years.

4. *species with inconsistent occurrence and abundance.* We collected high number of individuals (31) of the species *Calosoma sycophanta* (Linnaeus, 1758) in 2005. Although we found *Carabus scheidleri* Panzer, 1799 in high number in 1993, the number of this species decreased during the following years.

Table 1. Identity and abundance of ground beetle species, collected in the different habitats in the Pilis Biosphere Reserve, Hungary, during the studied years (1985, 1986, 1993, 1994, 2005, 2006).

Species	Areas			Total catch
	Beech	Transition	Oak	
<i>Abax parallelepipedus</i> (Piller et Mitterpacher, 1783)	466	271	70	807
<i>Abax carinatus</i> (Duftschmid, 1812)	38	320	9	367
<i>Abax ovalis</i> (Duftschmid, 1812)	30	23	21	74
<i>Abax parallelulus</i> (Duftschmid, 1812)	6	16	2	24
<i>Amara convexior</i> Stephens, 1828	0	0	1	1
<i>Amara saphyrea</i> Dejean, 1828	0	0	1	1
<i>Aptinus bombarda</i> (Illinger, 1800)	2837	434	785	4056
<i>Bembidion</i> sp.	0	3	0	3
<i>Bembidion lampros</i> (Herbst, 1784)	0	12	0	12
<i>Brachinus explodens</i> Duftschmid, 1812	0	0	1	1
<i>Calathus fuscipes</i> (Goeze, 1777)	0	3	4	7
<i>Calosoma inquisitor</i> (Linnaeus, 1758)	3	0	7	10
<i>Calosoma sycophanta</i> (Linnaeus, 1758)	4	3	24	31
<i>Carabus convexus</i> Fabricius, 1775	4	20	37	61
<i>Carabus coriaceus</i> Linnaeus, 1758	41	82	31	154
<i>Carabus intricatus</i> Linnaeus, 1761	1	3	0	4
<i>Carabus nemoralis</i> O. F. Müller, 1764	79	66	79	224
<i>Carabus scheidleri</i> Panzer, 1799	28	300	129	457
<i>Carabus ullrichi</i> Germar, 1824	351	357	597	1305
<i>Carabus violaceus</i> Linnaeus, 1758	0	0	1	1
<i>Cychrus caraboides</i> (Linnaeus, 1758)	0	10	0	10
<i>Harpalus atratus</i> Latreille, 1804	3	6	2	11
<i>Harpalus marginellus</i> Dejean, 1828	0	9	0	9
<i>Harpalus pumilus</i> Sturm, 1818	1	0	0	1
<i>Harpalus rufipes</i> (De Geer, 1774)	0	16	2	18
<i>Leistus rufomarginatus</i> (Duftschmid, 1812)	42	6	4	52
<i>Licinus hoffmannseggi</i> (Panzer, 1797)	0	1	0	1
<i>Molops piceus</i> (Panzer, 1793)	27	16	26	69
<i>Nebria brevicollis</i> (Fabricius, 1792)	2	48	0	50
<i>Notiophilus rufipes</i> Curtis, 1829	10	3	41	54
<i>Platynus assimilis</i> (Paykull, 1790)	163	1909	89	2161
<i>Platynus dorsalis</i> (Pontoppidan, 1763)	3	1	4	8
<i>Platyderus rufus</i> (Duftschmid, 1812)	0	1	0	1
<i>Pterostichus melas</i> (Creutzer, 1799)	61	61	1864	1986
<i>Pterostichus melanarius</i> (Illinger, 1789)	272	594	18	884
<i>Pterostichus niger</i> (Schaller, 1783)	1	39	0	40
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	94	538	55	687
<i>Pterostichus ovoideus</i> (Sturm, 1824)	3	58	2	63
<i>Pterostichus strenuus</i> (Panzer, 1797)	0	3	0	3
<i>Pterostichus vernalis</i> (Panzer, 1796)	0	9	0	9
<i>Stomis pumicatus</i> (Panzer, 1796)	6	3	0	9
<i>Synuchus vivalis</i> (Illinger, 1789)	2	6	3	11
<i>Trechus pilisensis</i> Csiki, 1918	5	102	0	107
Total	4579	5353	3912	13844

Table 2. Characteristics of carabid assemblages in the studied years (1985, 1986, 1993, 1994, 2005, 2006) in the Pilis Biosphere Reserve. Beech= beech forest; transition= transition zone; oak= oak forest.

years	areas						sum	
	beech		transition		oak			
	N. of species	N. of individuals	N. of species	N. of individuals	N. of species	N. of individuals		
1985	16	576	24	336	17	258	30	1170
1986	20	380	26	602	22	267	35	1249
1993	20	968	23	634	17	544	26	2146
1994	17	407	19	442	13	388	22	1237
2005	22	1202	22	1596	20	941	25	3739
2006	20	1046	29	1743	19	1514	32	4303

2.3.2 Diversity profiles

We found that the transition zone was the most diverse habitat in 1985-86, while the oak forest was more diverse than the beech forest (Figure 1). In 1993-94, we found a similar pattern in case of the diversity of rare species, where the beech forest was more diverse than the oak forest (Figure 2). The differences in Rényi diversity had disappeared by 2005-06, and the profiles became quite similar, except for the fact that the transition zone was the most diverse habitat for rare species (Figure 3). However, there was no clear difference in dominant species between the habitat types.

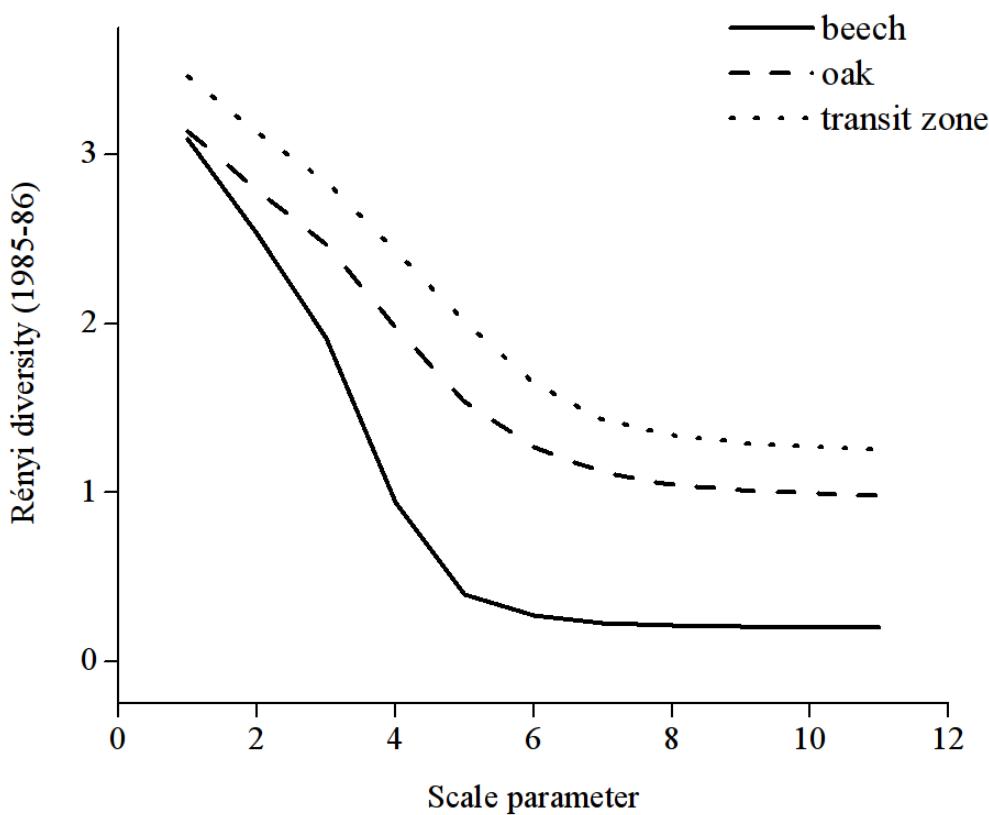


Figure 1. Diversity profiles of the carabid assemblages of the studied habitats in 1985-1986 in the Pilis Biosphere Reserve

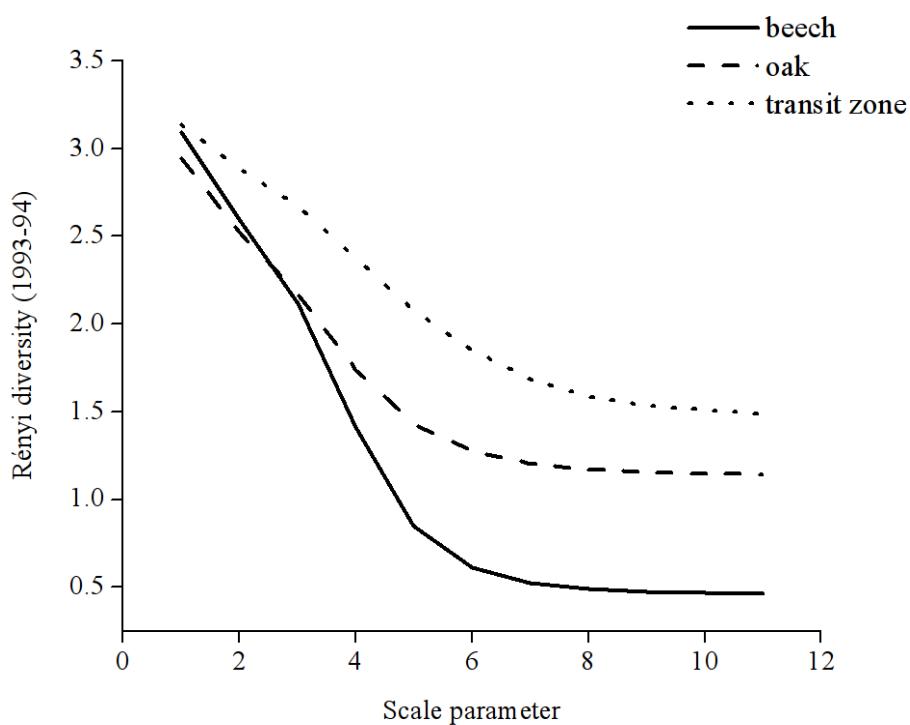


Figure 2. Diversity profiles of the carabid assemblages of the studied habitats in 1993-1994 in Pilis Biosphere Reserve

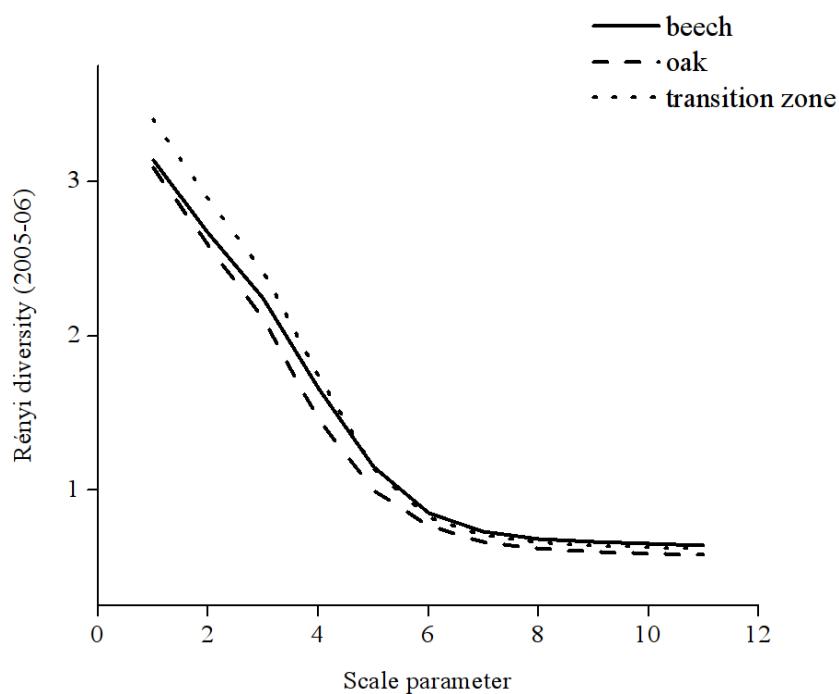


Figure 3. Diversity profiles of the carabid assemblages of the studied habitats in 2005-2006 in the Pilis Biosphere Reserve

2.3.3 Overall species composition

We found that there were significant differences among the years based on the species composition, especially between years 1985 and 1986 ($r=0.8$, $p<0.0001$), 1985 and 2005 ($r=0.76$, $p<0.0001$), 1985 and 2006 ($r=0.71$, $p<0.0001$), 1986 and 2005 ($r=0.79$, $p<0.0001$), 1986 and 2006 ($r=0.74$, $p<0.0001$), and 2005 and 2006 ($r=0.88$, $p<0.0001$) without regard to habitat types (Table 3).

Table 3. The comparison of species composition by Mantel test, Pilis Biosphere Reserve, 1985-2006

Comparisons	Pearson's R	p
1985-86	0.8	0.00009
1985-93	0.6	0.00009
1985-94	0.57	0.0001
1985-2005	0.76	0.00009
1985-2006	0.71	0.00009
1986-93	0.52	0.00009
1986-94	0.48	0.0004
1986-2005	0.79	0.00009
1986-2006	0.74	0.00009
1993-94	0.65	0.00009
1993-2005	0.58	0.00009
1993-2006	0.61	0.00009
1994-2005	0.64	0.00009
1994-2006	0.64	0.0002
2005-06	0.88	0.00009

2.3.4 Investigation of characteristic species

Based on the IndVal procedure (Table 4) we identified four groups of species: 1) species of beech forest; 2) species of transition zone; 3) species of transition zone and oak forest; 4) species of oak forest. During the years, we found particular variation among the habitats based on the presence of characteristic species. The beech forest had no characteristic species in 1986 and 2006, while the rest of the years the *L. rufomarginatus* was typical except in 1994, when the *Pt. oblongopunctatus* was typical in this habitat. The transition zone contained characteristic species in all years with considerable variation in the species composition during the time.

The group no. 3 was supported by one indicator species in 1985 (*C. scheidleri*) and 1994 (*C. convexus*). In the oak forest *Pt. melas* and *N. rufipes* were typical during the years, except in 1993 and 2006, when no characteristic species were found.

Table 4. The characteristic species of the studied habitats in the Pilis Biosphere Reserve, 1985-2006. Figures in the brackets denotes the IndVal value for the given species.

Years	Beech	Transition	Transition+oak	Oak
1985	<i>Leistus rufomarginatus</i> (60)	<i>Trechus pilisensis</i> (100), <i>Harpalus rufipes</i> (88.89), <i>Pt. vernalis</i> (80), <i>Pt. niger</i> (77.33), <i>Abax parallelepipedus</i> (76.32), <i>Pt. melanarius</i> (72.84)	<i>Carabus scheidleri</i> (75.29)	<i>Pt. melas</i> (91.03)
1986	No species	<i>T. pilisensis</i> (100), <i>Abax carinatus</i> (86.67), <i>Pt. melanarius</i> (85.37), <i>Pt. oblongopunctatus</i> (83.53), <i>Carabus coriaceus</i> (65.45)	No species	<i>Pt. melas</i> (86.57), <i>Notiophilus rufipes</i> (81.82)
1993	<i>L. rufomarginatus</i> (93.33)	<i>Pt. melanarius</i> (88.79), <i>Pterostichus ovoideus</i> (87.5), <i>A. carinatus</i> (87.27), <i>Platynus assimilis</i> (85.37)	No species	No species
1994	<i>P. oblongopunctatus</i> (85.11)	<i>A. carinatus</i> (100), <i>Pl. assimilis</i> (83.91), <i>Pt. melanarius</i> (80.77)	<i>Carabus convexus</i> (85.71)	<i>Pt. melas</i> (91.36)
2005	<i>L. rufomarginatus</i> (62.61)	<i>Pt. oblongopunctatus</i> (93.43), <i>Pl. assimilis</i> (89.63)	No species	<i>N. rufipes</i> (75)
2006	No species	<i>Nebria brevicollis</i> (100), <i>T. pilisensis</i> (100), <i>Pt. ovoideus</i> (96.88), <i>A. carinatus</i> (92.2)	<i>Pt. melas</i> (98.71), <i>Pl. assimilis</i> (95.21)	No species

Pt.: *Pterostichus*; Pl.: *Platynus*

2.3.5 Body-size categories and habitat affinity categories by habitat types and years

On the basis of the body-size of carabid species three groups were distinguished: small, medium-sized and large beetles as it was described in details in part 2.2.2. In case of small species we did not find particular differences in the transition zone among the years. The small species were found mostly in the two forests and occurred in low numbers in the transition zone. As far as the oak forest is concerned, there was a significant increase by 2005-2006 most likely due to the high numbers of *Pt. melas*. In the beech forest we found significant changes among the years, and these fluctuations were likely associated to *Ap. bombardata*. In case of the medium-sized species however we found some of these species in all areas, they occurred mainly in the transition zone in 2005-06, which was highly associated to the high number of individuals of *Pt. oblongopunctatus*, *Pl. assimilis* and *Pt. melanarius*. We found that the abundance of large carabids, such as *C. ullrichi*, *C. coriaceus* and *C. violaceus* increased during the years in the two forest areas. In the years 1985 and 1986 the large *Carabus* species preferred the transition zone. We found significant increase in their abundance between 1985 and 2006 in the transition zone, however their numbers did not change significantly among the years 1993, 1994 and 2005 (Figure 5).

Three groups of ground beetles were identified by the literature data (Lindroth 1985, 1986; Hürka 1996) concerning on the habitat affinity of the species described in details in part 2.2.2: 1) forest species; 2) habitat generalists occurring in both habitats; and 3) open-habitat species. The last group includes species occurring mostly in the transition zone. There is variability in the abundance of forest species particularly in 2005 and 2006 in the transition zone. There was no significant difference among the habitats concerning the abundance of generalist species, even if there was a particular increasing tendency of it in all habitats by 2005 and 2006. Although the number of generalist species was always the highest in the transition zone, the number of individuals in this group was the highest in the oak forest in all years, except in 1986. By the year 2006 this number increased significantly, as a consequence of the growing presence of *Pt. melas*. In all habitats, the abundance of open-habitat species, such as some *Harpalus* species, increased significantly during the years (Figure 6).

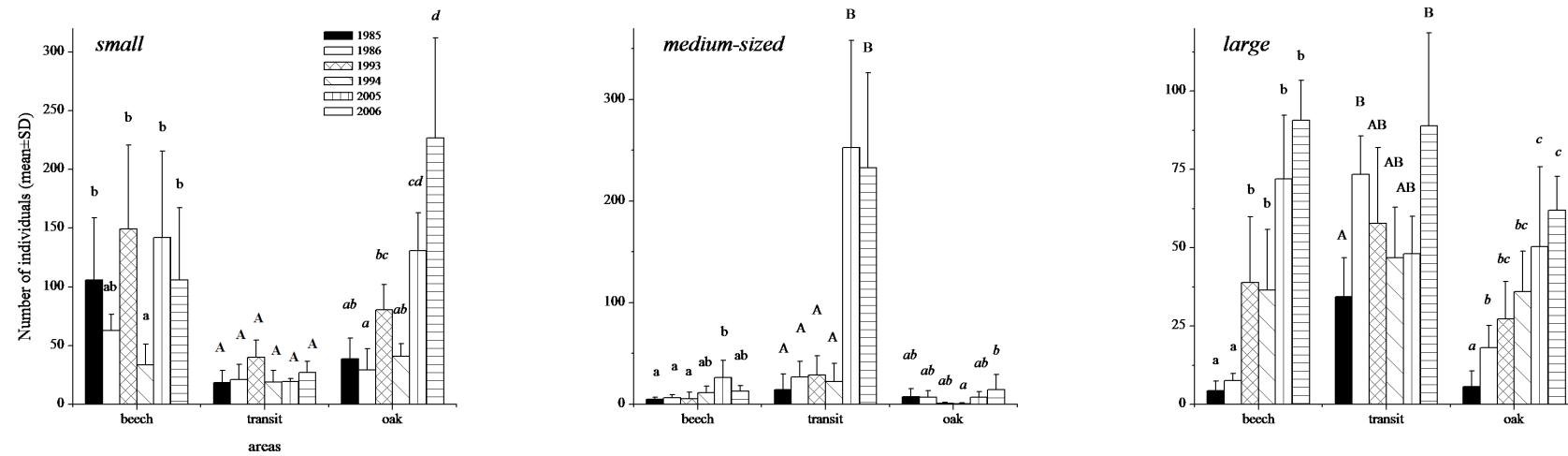


Figure 5. The distribution of small, medium-sized and large species in three habitats and in all years in the Pilis Biosphere Reserve. (Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

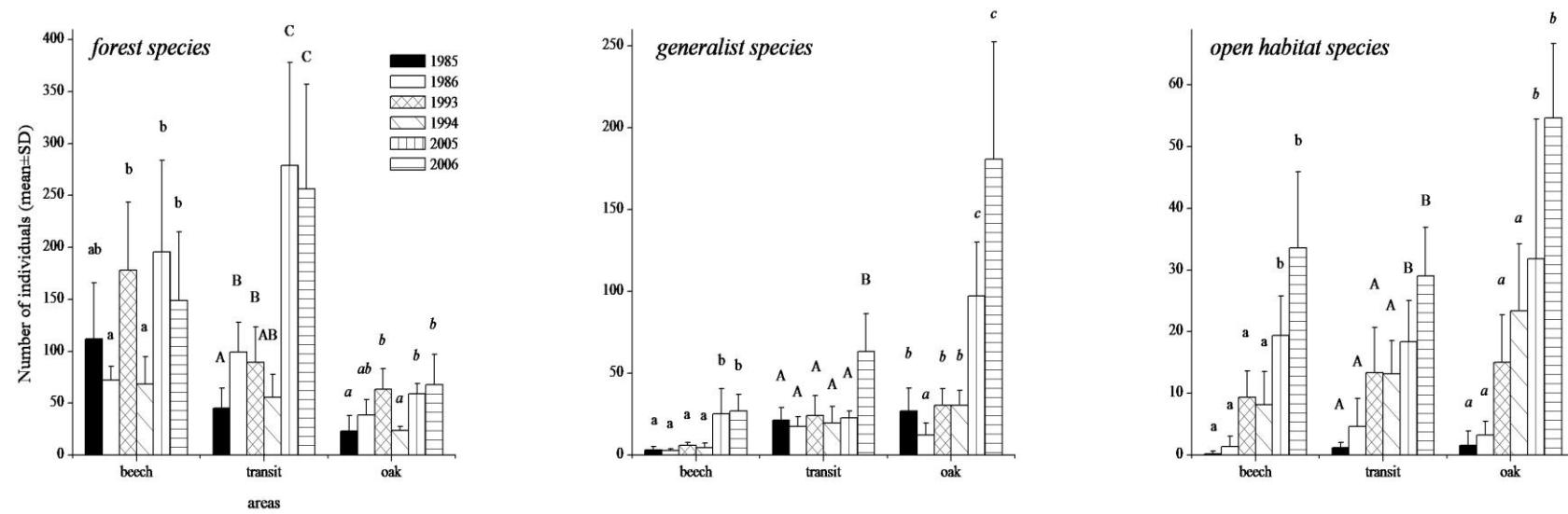


Figure 6. The distribution of forest specialist, habitat generalist and open-habitat preferring carabid species in three habitats and in all years in the Pilis Biosphere Reserve. (Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

2.3.6 Species-specific responses

The results of species-specific responses (i.e. how individual species abundances changed over years) are summarized in the Table 5, and portrayed in Figures 7, 8, 9, and 10. Present in all areas and in all years, *Ap. bombarda* preferred the beech forest, with particular fluctuations among the consecutive years. Similarly, *A. parallelepipedus* showed a significantly increasing number of individuals through the years mostly in the beech forest. This species also occurred in high number in the transition zone and we also found some individuals in the oak forest; however the number of individuals did not show remarkable differences throughout the years. Although being present in all areas, *Pt. melas* preferred the oak forest, and the number of individuals of this species increased significantly by 2005 and 2006. *Pt. melanarius* occurred both in the transition zone and in the beech forest, and its abundance increased over the years, significantly by 2005 and 2006. *Pl. assimilis* was strongly associated with the transition zone; it was represented especially with high number of individuals in 2005 and 2006. Similarly to *Pl. assimilis*, *Pt. oblongopunctatus* showed the same preferences and similar variation in time. *C. scheidleri* occurred in high number especially in the transition zone in 1986. The number of this species decreased during the following years. Contrary to *C. scheidleri*, the abundance of *C. ullrichi* remarkably increased through the years in all areas, especially in the oak forest.

Table 5. Results of the species modelling in the studied sites in the Pilis Biosphere Reserve, in 1985-86, 1993-94, 2005-2006. Based on the number of individuals caught, the modelling determines the direction of abundance change of a species over a time period and in a habitat type.

species	Estimated values (slopes) with \pm S.E.			
	beech	transition	oak	comparison
<i>Abax parallelepipedus</i>	0.04 \pm 0.09	-0.17 \pm 0.04	-0.31 \pm 0.06	B>T***; B>O***
<i>Aptinus bombarda</i>	0.74 \pm 0.05	-0.58 \pm 0.04	-0.44 \pm 0.04	B>O***; B>T***; O>T*
<i>Carabus scheidleri</i>	-0.68 \pm 0.12	0.73 \pm 0.09	0.46 \pm 0.1	O>B***; T>B***; T>O***
<i>Carabus ulrichi</i>	-0.34 \pm 0.16	-0.01 \pm 0.05	0.16 \pm 0.05	O>B**; O>T**
<i>Platynus assimilis</i>	-0.33 \pm 0.13	0.54 \pm 0.07	-0.08 \pm 0.1	T>B***; T>O***
<i>Pterostichus melas</i>	-0.31 \pm 0.11	-0.16 \pm 0.13	0.64 \pm 0.09	O>B***; O>T***
<i>Pterostichus oblongopunctatus</i>	-0.17 \pm 0.11	0.23 \pm 0.08	-0.05 \pm 0.12	T>B*; T>O*
<i>Pterostichus melanarius</i>	0.04 \pm 0.1	0.17 \pm 0.06	-0.16 \pm 0.16	T>B*

* p<0.05; ** p<0.01; *** p<0.001. Beech and B= beech forest; transition and T= transition zone; oak and O= oak forest.

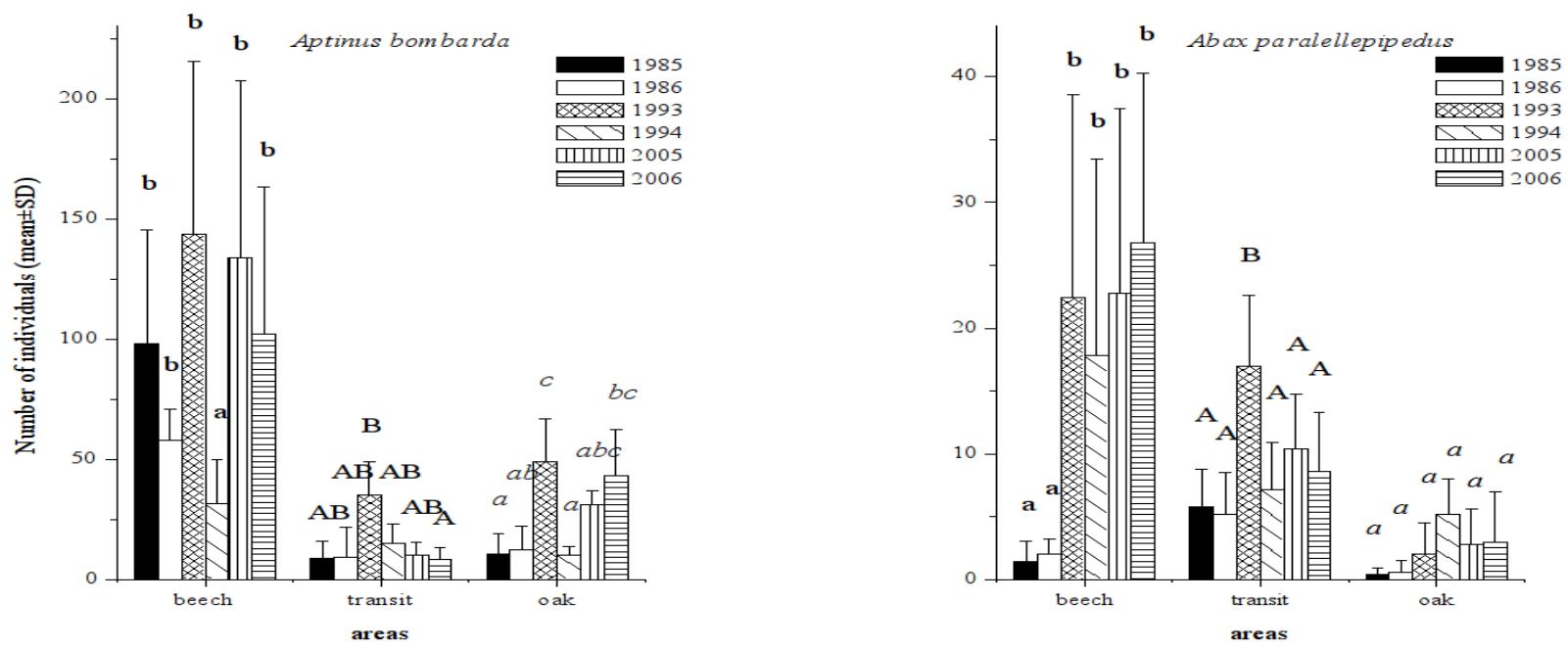


Figure 7. The habitat affinity of *Aptinus bombarda* and *Abax parallelepipedus* in the Pilis Biosphere Reserve in all the studied years. (Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

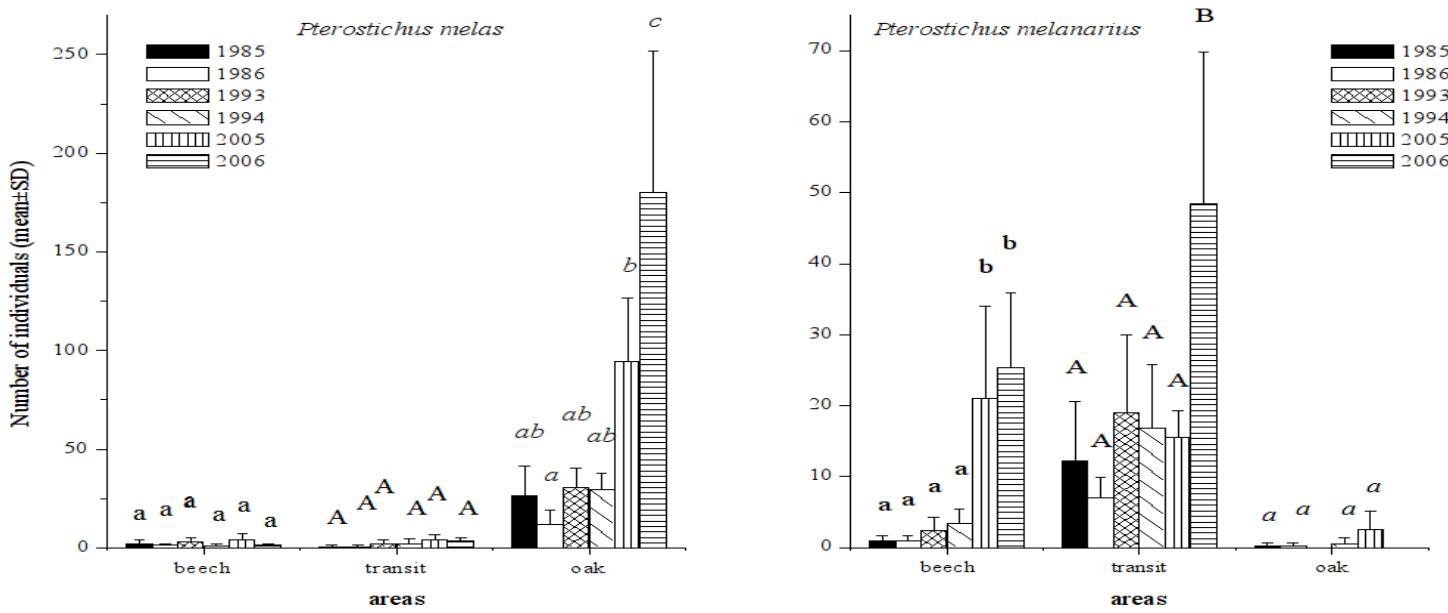


Figure 8. The habitat affinity of *Pterostichus melas* and *Pterostichus melanarius* in the Pilis Biosphere Reserve in all the studied years. (Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

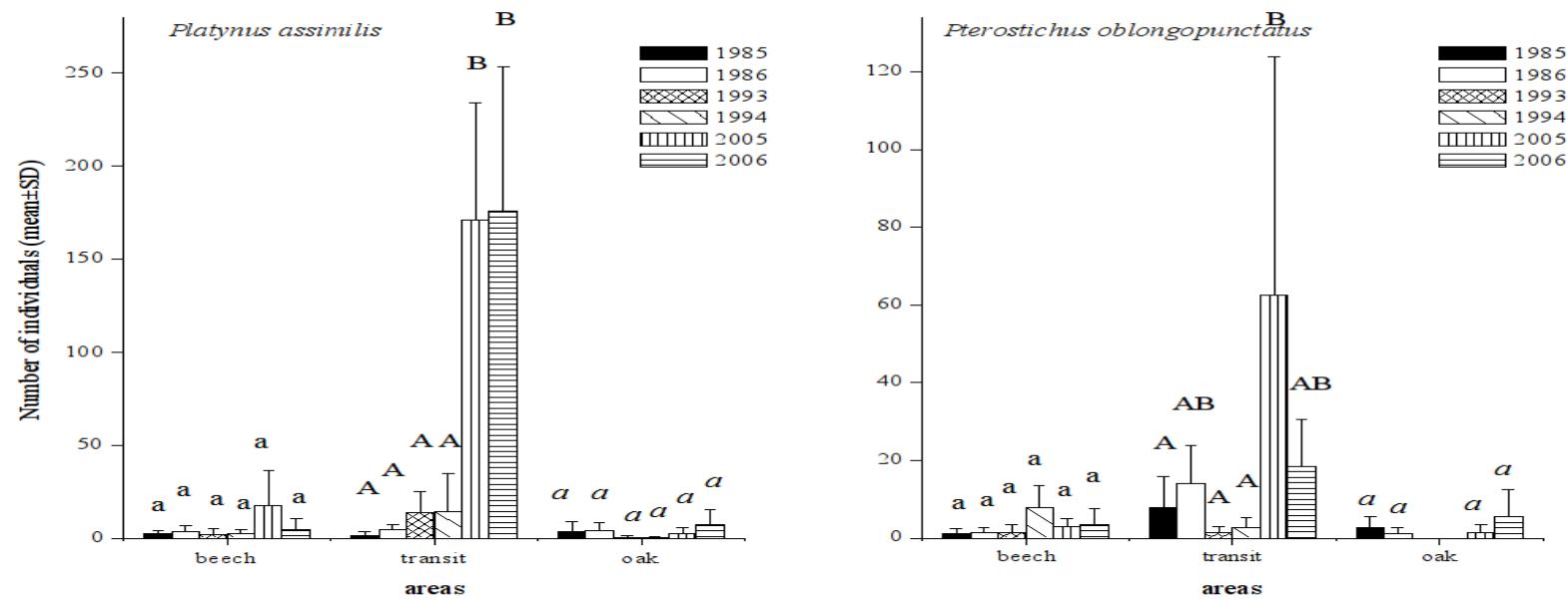


Figure 9. The habitat affinity of *Platynus assimilis* and *Pterostichus oblongopunctatus* in the Pilis Biosphere Reserve in all the studied years.
(Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

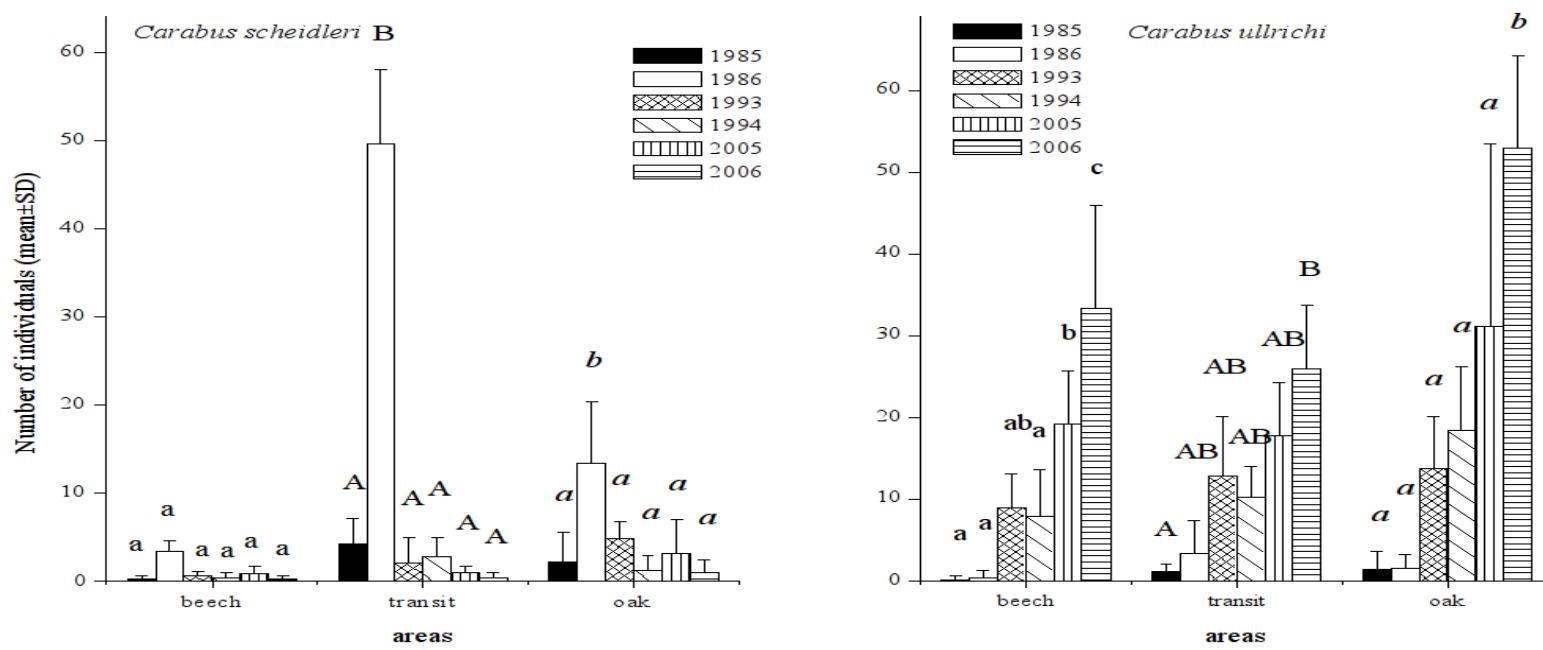


Figure 10. The habitat affinity of *Carabus ullrichi* and *Carabus scheidleri* in the Pilis Biosphere Reserve in all the studied years. (Different letters indicate significant ($p<0.05$) differences between years within a habitat type by Fisher's *post-hoc* LSD test.)

2.4 Discussion

Our study proved that there is a remarkable change in the species composition and activity density of ground beetles in this investigated area. Similarly to Grüm (1984) we found that the flightless large forest carabids are the most sensitive to the forest management because of their limited dispersal power and lower fecundity (Figure 5). We found that after twenty years the large *Carabus* species had higher abundance in all habitat types. Thus, their monitoring might be a good indicator of environmental changes. The composition and the occurrence of carabid species in PBR were initially investigated between 1982 and 1984 at landscape scale (Kádár & Szél 1999). This study prompted us to develop new approaches such as a small-scale study, where the soil moisture was assumed as an important determinant of carabid distribution (*sensu* Thiele 1977; Epstein & Kulman 1990). Forest carabid species prefer microsites with a particular kind of environment heterogeneity, as favourable microclimate (soil temperature, ground air temperature, and relative air moisture), the presence of dead and decaying trees, cover of leaf litter, shrubs and herbs (Desender et al. 1999). Other biotic and abiotic ecological factors also influence the composition of the carabid assemblages and distribution of the species, like soil pH, soil compactness, CaCO₃ content of the soil, as well as the type and amount of preys (Magura et al. 2002).

Our results suggest that ground beetle assemblages may reflect the small scale spatial heterogeneity among the different habitat types through the specific responses of some species, but most of the species use these habitats regardless the spatial variations. Based on our results, there are at least two important points that prove the above statement: 1) the overall abundance and species richness were the highest in the transition zone (Table 2); 2) most of the species were characteristic of all habitat types; only few species was specific to any one habitat (Table 4). The IndVal results (Table 5) showed that only a few species were considered as characteristic species of the transition zone and the oak forest. However, the abundance of certain species (*Pt. melas*, Figure 8) varied among the habitats sufficiently and the species also reacted to the environmental changes, some species distinguished the habitats by occurring in higher number in the preferred habitat (*C. ullrichi*, Figure 10). But they also used the other habitats at the same time. These patterns might support the concept of metacommunity theory, wherein species interact by affecting each other's demographic rates

and a metacommunity as a set of local communities that exchange colonists of multiple species through dispersal (Leibold et al. 2004).

According to our results the species richness and the activity density were lower in the dry oak forest, than in the humid transition zone and beech forest (Table 2 and Kádár et al. 2013). The diversities of the carabid assemblages in the beech forest were always the lowest. The diversity was always the highest in the transition zone during all years. This zone is occupied by species characteristic of both adjacent habitats, thus, it explains the high species richness of this site. The observed pattern in diversity (i.e. transition zone being the most diverse habitat) can be the consequence of the high evenness in this habitat. A similar pattern in species richness and activity density was described in ground-dwelling spiders by Liu et al. (2002). Our results can also be explained by the local attributes of vegetation (such as canopy closure) or by geographical features (such as terrain slope). Ewers and Didham (2006) also showed that habitat edges are hyper-dynamic ecological systems (i.e. high abundance and species turn-over), resulting in the destabilization of animal populations. The ground beetles probably use these habitats during dispersal, between the hibernating and reproducing sites (Bommarco & Fagan 2002). Small-scale movements of carabids between the habitats might affect ground beetle assemblages in the adjacent habitat patches (Niemelä & Halme 1992). That is why the number of species increases and their relative abundances alter in the adjacent habitats. Thus, the transition zones might be also considered as a source of the diversity of carabid communities in the neighbouring habitats.

The thinning as a forest management which was implemented before our study, was likely to highly influence the composition of the carabid assemblages inhabiting the area. However, the abundance of ground beetle species in all habitats increased throughout the years, the species richness in all habitats did not differ (Figure 3), which shows that the majority of the species was present in low abundance right after the initiation of the forestry practices, but they subsequently tended to recover. Ten years after the completion of the forest practices (in the years of 1990s), we found significant differences neither in the abundance, nor in the species composition in the carabid assemblages. However, twenty years after the forest management (in 2005 and 2006), we found significant increases in the number of the majority of the large forest carabids, which might be the indicator of the naturalness of these habitats. All these indicate the remarkable resilience of the carabid populations.

We showed the following types of carabid beetle responses in the recovering habitats from forestry practices: 1) forest species persisted throughout the studied years; the number of their individuals increased significantly by the years of 2005 and 2006. Their high abundance showed that the habitat quality has improved due to high amount of prey (Kádár et al. 2013), which fully concurs with the fact that there was a gypsy moth, *Lymantria dispar* (Lepidoptera, Erebidae) gradation during these years (Kádár pers. comm.); 2) generalist species showed significant abundance increases only in the last two studied years in all habitats, thus these species spread out twenty years later after the forest management halted; 3) open-habitat species appeared and increased in abundance, particularly in the oak forest, however, these species did not disappear when the canopy closed.

The increasing number of the individuals of small body sized species in the oak forest (Figure 5) suggests that these species occurred and preferred the more opened oak habitat contrary to the beech forest and the transition zone. In the transition zone the medium-sized ground beetle species increased by 2005 and 2006, which is associated with the increasing presence of *Pt. oblongopunctatus* and *Pl. assimilis*. In the case of the large carabid species, their growing numbers in all habitats can be attributed mostly to *Carabus* species increasingly present in the last two years, indicating the stability of these habitats. These differences in the overall abundance and species richness are due to the specific habitat requirement of each species (e.g. Ulyshen et al. 2006).

All of the abundant species showed preferences to habitats. The beech forest was dominated by three species, *Ap. bombarda*, *A. parallelepipedus* and *Pt. melanarius* in the last two studied years (Figures 7 and 8). These species were present in all years with fluctuating abundances, indicating that the forest practices disturbed neither the presence nor the preference of this species. The distribution of the *Ap. bombarda* in Europe is well known (Brandmayr 1974; Casale & Vigna Taglianti 1983; Pravisan & Torossi 1987; Fazekas et al. 1992). However, in Italy, this species was found only in *Seslerio-Quercetum*, and even with an extremely high dominance value (Brandmayr et al. 1980), it is a typical forest-dwelling species in Hungary (Kádár & Szél 1993) and in our study it preferred the beech forest, similarly to Magura et al.'s (2002) investigation. The second most abundant species in the beech forest was *A. parallelepipedus*, which was nearly absent in the 1980s (Figure 7). In spite of the persistence in low number of individuals of this species, it spread out the following years, probably because of the cessation of the forest management becoming a subdominant species in this

habitat. There were more individuals in the beech forest in the years of 1990s, but this is an ambiguous conclusion, because of the lack of the permanent survey between the years of 1980s and the years of 1990s. The natural fluctuation of *A. parallelepipedus* population could be another reason behind this phenomenon. It is a common species, and well-adapted to each environmental condition, but its distribution might change at larger spatial scale, for example following a forest management period (Loreau & Nolf 1994). That might have happened in our study site too. *A. parallelepipedus* was also among the most abundant species captured in the different sites in the studies of Kdr & Szl (1993, 1999), and Magura et al. (2002). This carabid is a typically opportunistic species, and has a good adaptation strategy to the overall environment (Kdr & Szl 1993). That is why it is a dominant species in different habitats (Chemini & Werth 1982, Contarini 1986, Pravislani & Torossi 1987). Similarly, *Pt. melanarius* surviving the disturbances reoccurred in high number not only in the beech forest, but mainly in the transition zone (Figure 8). This means that the quality of this zone also ameliorated. In our study, *Pt. melanarius* preferred the transition zone, i.e. preferred the habitats with high level of the soil moisture and dense shrub vegetation. It can be found in relative high numbers in quite different habitats, for example, it is also a common species of the agricultural landscapes (Thiele 1977) and river side woodlands (Baguette 1993). *Pt. melanarius* occurred in high numbers in all environment types, like fields, pastures, abandoned fields and also in forests examined by Niemel & Halme (1992) in Finland. Although the species is favoured by human activity, our study and that of Niemel & Spence (1991) also showed that it was not restricted only to disturbed habitats.

In the transition zone, although at first in 1985 poorly represented by number of individuals, in 2005 two major species appeared in great numbers, *Pt. oblongopunctatus* and *Pl. assimilis* (Figure 9). *Pl. assimilis* was also found in the PBR between 1982 and 1984 (Kádár & Szél 1999), but it was not as abundant a species, as it was during the years studied by us. Similarly to our study, it is reported to occur in wet, shady forests (Kleinert 1983).

Slovakia (Kleinert 1983). This species appeared as soon as *C. scheidleri* disappeared from the habitats. *C. scheidleri* prefers the disturbed, human-modified areas (Andorkó & Kádár 2009), that is why this species was found in high numbers in 1986, and it was hardly found by the years of 1990s. As mentioned above *C. ullrichi* occurs in more stable forests. That might be the reason of the distribution of this species in the years of 1990s.

To be useful in conservation, an indicator must have high and consistent predictive power that relates to particular conditions (Koivula 2011). However, most of the groups that could be indicator organisms have not been subjected to a critical assessment using set criteria (Pearson & Cassola 1992). According to Lövei (2008) once we develop the criteria set out in Pearson & Cassola (1992), we can realistically assess the suitability of ground beetles as indicator organisms. We still lack all the information showing carabids to reliably predict entities of high conservation and management interest. According to Koivula (2011) in order to fill this gap firstly knowledge on the relationship between carabids and other taxa must be greatly increased, and afterwards strict test must be applied to evaluate indicator function. However, carabid beetles might be appropriate indicators of site and site conservations (*sensu* Eyre & Rushton 1989).

3 Section II. - Life-history characteristics of two *Carabus* species

3.1 Introduction

Knowledge of the biology of the study organisms in ecology is essential. Therefore it is necessary for an ecologist to contribute to our lack of knowledge on life histories (Lövei 2008). According to Allison et al. (1997) the current situation is this: a large proportion of the known arthropods are represented in collections by a single specimen (singletons), about which we know nothing except the location of its single occurrence and species name.

Most of the recent papers concentrate on processes at community level using mechanistic modelling of habitat alterations (Niemelä 2001; Niemelä et al. 2007; Martinez et al. 2009), and only few papers are concerned with the life-history traits and reproduction of carabids (Barbaro & van Halden 2009). However, sometimes the classical elements of species attributes such as life-history characteristics provide clues for conservation of biodiversity.

Life-history theory attempts to understand how natural selection designs organisms to achieve reproductive success, given knowledge of how selective factors in the environment (i.e., extrinsic mortality) and factors intrinsic to the organism (i.e., trade-offs, constraints) affect survival and reproduction (Fabian & Flatt 2012). The principal aim of life-history theory, a branch of evolutionary ecology, is to explain the remarkable diversity in life-histories among species (Fabian & Flatt 2012). But there is another, more compelling reason for why life-history evolution is important: adaptation by natural selection is based on variation in Darwinian fitness among individuals, and since life-history traits determine survival and reproduction they are the major components of fitness. The study of life-history evolution is thus about understanding adaptation, the most fundamental issue in evolutionary biology (Fabian & Flatt 2012). Together, the age-, size-, or stage-specific patterns of development, growth, maturation, reproduction, survival, and lifespan define an organism's life-cycle, its life-history (Stearns 1992). Using life-history traits for ecological assessments might be beneficial due to the fact that these reflect better to the local environmental parameters than species richness and abundance. These adaptations can be morphological or behavioural which makes these traits more suitable to track any changes in their environment (Nylin & Gotthard 1998). Life-history biologists have already provided some compelling answers to

fundamental questions by testing these major life-history traits in field and if possible, also in laboratory experiments, for example in flies, fish, or birds, and also in carabids (Fabian & Flatt 2012). During our studies we examined the life-history characteristics such as the seasonal activity, the age-composition and some reproductive characteristics of two ground beetle species.

Carabids are holometabolous insects that usually lay their eggs singly (Thiele 1977). Some species lay eggs in small or larger batches in crevices or in the soil after a varying degree of preparatory work by the female (Luff 1982; Thiele 1977). According to Brandmayr & Zettler-Brandmayr (1979) the female carefully chooses the ovipositing site, sometimes excavating a chamber for the eggs. The typical carabid larva is free moving and campodeiform (Crowson 1981) and usually undergoes three stages before pupating in a specially constructed pupal chamber in the soil. Some species (for example, *Harpalus* and *Amara* spp.) have only two larval stages. The larvae (second or third stage) of many species undergo diapause, either hibernation or aestivation. Sclerotisation and coloration of the adult takes place after eclosion; teneral beetles can be recognized for various lengths of time, usually weeks (Lövei 2008).

Understanding of the life-cycles of even common carabid species has accumulated only slowly, generally from observations of population activity in the field. Larsson (1939) distinguished three different reproductive types in carabids:

- *autumn-breeders*, which reproduce in autumn or even from the height of summer onwards and usually hibernate as larvae;
- *spring breeders with autumn activity*, which hibernate as adults and reproduce from spring to early summer, after which most of the beetles die off, and the new adult generation appears in autumn, become fully active, although only reproduces next year following hibernation; and
- *spring breeders without autumn activity*, which reproduce in the same time as the other spring breeders, but the young beetles exhibit little activity following eclosion in autumn. They differ from each other in seasonal development and reproduction.

Lindroth (1949) recognised the over-simplicity of this division and suggested the use of the alternative and more general terms: adult hibernator and larval hibernator. However, other investigations have shown that not only the larvae, but also the adults of autumn breeders may hibernate, after which they can enter a second reproductive period (Gilbert 1956; Vlijm et al.

1968; van Dijk 1972). So far, the existence of two populations even of the same species side by side, the one reproducing in spring and the other in autumn was found by Schjøtz-Christensen (1965), and by Löser (1970). This finding is an explicit example of two different life-history strategies within the same species. Thiele (1977) recognised that carabid life-cycles could be much more complicated than either of these simple classifications. According to Thiele (1977) both time of oviposition and the overwintering instar had to be considered in classifying life-cycles. He suggested a division of species into five types distinguishing (a) spring breeders with summer larvae and hibernating as adults; (b) two distinct types of autumn breeders: one, comprising species with winter larvae and adults reproducing from summer to autumn without adult dormancy, and (c) a second, grouping species having winter larvae and adults emerging in spring with dormancy before reproduction; (d) a group he described as having 'flexible' reproductive periods, and (e) a final group characteristic of high latitudes which required more than one season to complete development. Paarmann (1986) elaborated this system even further, additionally distinguishing two types of spring breeders and two types of extended multi-season developments on the basis of a more mechanistic understanding of environmental control during periods of dormancy gained from his own and a number of other laboratory studies. Several field studies concerning the phenology of individual species support Thiele's view that carabids exhibit more complex life-cycles than had been previously recognised. Since Thiele's classification provided the most possibilities to classify the species into one group, firstly we considered it to be relevant in our cases.

However, according to Matalin (2007) the classification is based on a combination of five criteria: duration, number of generations per season, phenology of reproduction, stability, and repeatability of reproduction. According to the individual lifespan, the cycles are subdivided into annual and biennial ones. The annual life-cycles may be uni- and bivoltine, whereas biennial ones are always univoltine. By the time of reproduction, winter-spring, spring, spring-summer, early summer, summer, late summer, summer-autumnal, autumnal, autumn-winter, winter, and aseasonal species are distinguished. The biennial and bivoltine cycles may be of both facultative and obligate nature (Matalin 2007). Species living only one season and having a continuous reproductive period are designated as semelparous, while those breeding during two or more years or having several distinct periods of reproduction in one season, are iteroparous. Repeated similarly directed modifications of the life-cycle may produce essentially different seasonal rhythms in some individuals. In this case, two subpopulation groups usually appear within the population. Under the most unfavorable conditions, these

groups become practically isolated and hibernate at different ontogenetic stages. The individual development in each of these groups takes two years with the same seasonal rhythm. Among the types considered, only obligate-bivoltine life-cycles are always polyvariant, but annual univoltine and obligate-biennial ones are always univariant. The facultative-bivoltine and biennial life cycles may be realized as uni- and polyvariant ones, depending on the environmental conditions (Matalin 2007).

In general, ground beetles develop from egg to adult in less than one year, reproduce once, and perish. However, harsh climates or adverse food conditions might influence individual development lasting up to four years. Some examples presenting the diversity of life-cycles of carabids are the followings: 1) *C. glabratus*, a species with larval hibernation and autumn reproduction in central and western Europe, has a biennial life-cycle with spring breeding in upland areas of northern England (Houston 1981) and in Norway (Refseth 1984). 2) A population of *C. problematicus* in northern England has an annual life-cycle below 800m and a biennial one above that altitude (Butterfield 1986). 3) *C. auronitens* living in Europe has a flexible life-history strategy (*sensu* Thiele 1977) (opportunistic oviposition, asynchronous development, partial survival of the old generation, fat body reserves, and long-term dormancy). These life-trait characteristics reduce the risk of the whole population being affected by bad weather during the postecdysial ripening (Weber & Klenner 1987). Adult longevity can also exceed one season. There are several examples found from different parts of the world, for example, Europe (Gergely & Lövei 1987, Houston 1981, Luff 1982), Japan (Sota 1984), and the sub-Antarctic (Davies 1987), where species can live up to four years and reproduce more than once (Lövei 2008). In summary, several species show plasticity of individual development, whereas others seem to have a stable life-cycle. Furthermore, obligatory univoltism is apparently rare and occurs mainly in species of short longevity. Bi- and multiannual cycles are usually found in species living in harsh environments (sub-Arctic, highland, or xeroterm habitats), and dynamic polyvariance is common.

According to Grüm (1984) autumn breeders had higher egg numbers than spring breeders, and egg-laying rates were inversely correlated with female mobility. These results, along with observations of low egg numbers in cave-inhabiting species (Deleurance & Deleurance 1964) and of species demonstrating parental care in Europe and New Zealand (Brandmayr & Zettler-Brandmayr 1979), conform to some predictions of the r and K strategies theory. Also, ground beetle species living in unstable habitats have higher egg numbers than relatives living under

less variable conditions (Lövei 2008). Grüm (1984) observed similar differences in adult life spans and egg numbers among the Polish and Dutch populations of several species. However, the r-K theory is only one of the hypotheses suggested to explain life-history features.

Establishing the natural life-cycles of invertebrates is not a routine task. Whilst this may be straightforward for species with an obvious annual life-cycle, the problem becomes more difficult for species with greater longevity (Sparks et al. 1995). An accurate method would be to undertake a large-scale mark-recapture programme where released individuals were of a known age. Such a method requires considerable inputs of time and of labour and may take several years to achieve results. Alternative methods for ageing are presented in several literatures (Butterfield 1986; Houston 1981; van Dijk 1972, 1979; Wallin 1989; Diefenbach et al. 1991). These authors suggested mandible condition, i.e. wearing, as an indication of the relative age of the individuals and supplemented this information with assessments of sexual maturity. The basic assumption was that mandible wearing would be related to food consumption and hence positively correlated to age. Houston (1981) relied largely on mandible condition and established a four-grade wearing scale, whilst Butterfield (1986), in an assessment over different altitude sites, measured the length of the mandible tip.

The method used by Houston (1981) relied on a subjective score for mandible condition. A similar measure was taken in the study of Sparks et al. (1995), however, it has been used for illustration only and not for age estimation. In our studies ageing was firstly based on the length and extent of bristles (several rigid setae extruding between the clypeus and labrum) and on mandible wear, hardness and coloration of elytra (van Dijk 1972; 1979). In addition we also dissected the females in order to determine the developmental stage of their ovaries and the number of eggs found in their ovaries, following the method of van Dijk (1972, 1979), Wallin (1989) and Diefenbach et al. (1991). We considered that the results of the dissections of the females could support the results of the age-estimation based on mandible wear and also could help achieve a more accurate age estimation (Andorkó et al. 2007). Unlike many other insects, there is evidence to suggest that carabids may reproduce more than once during their life-time as already mentioned above (Rijnsdorp 1980; Bérces & Elek 2012). Thus sexually mature beetles are not necessarily in their final year. Hence, we used both methods to achieve the more precise results of age estimation.

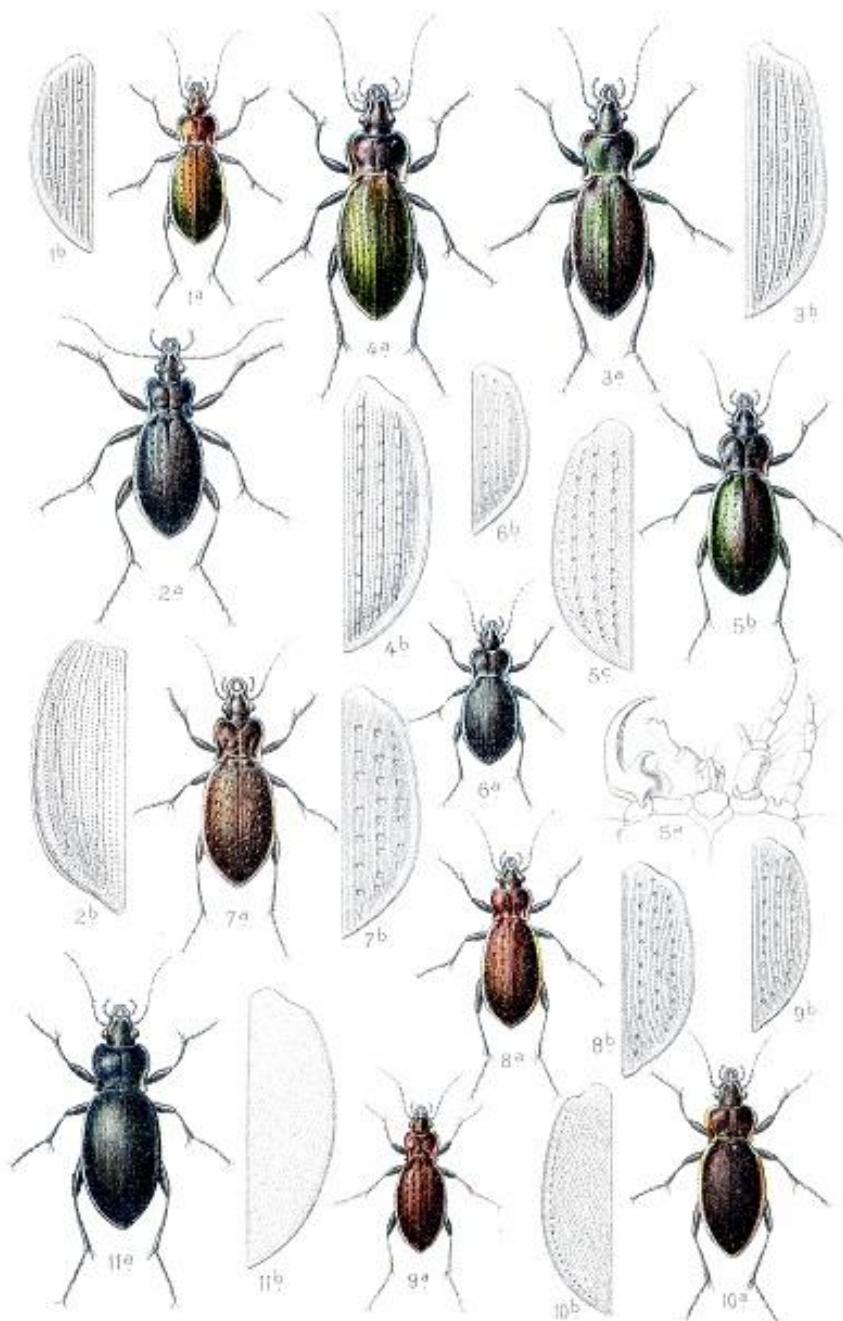
We chose two carabid species with sound differences in reproductive characteristics observed in the field, in order to determine whether only the ageing based on mandible wear gave adequate results of the real age of the beetles. We chose these two selected species according to their relevance of the Hungarian carabid fauna. *Carabus scheidleri* reflects well the environmental changes, so it can be used as an indicator organism; however, we have sparse information about the biology, population dynamics and the ecology in Hungary of this species (Andorkó et al. 2005). Contrary to *C. scheidleri*, *C. ullrichi* is a wide-spread, common and a typical spring-breeder species. In the course of the investigations in the PBR we found both species occurring in the same area (Andorkó & Kádár 2006). While *C. scheidleri* occurred in a high number in all areas in 1986, the number of this species decreased during the following years. To the contrary, the abundance of *C. ullrichi* remarkably increased through the years in all areas.

3.2 Materials and methods

3.2.1 Study species

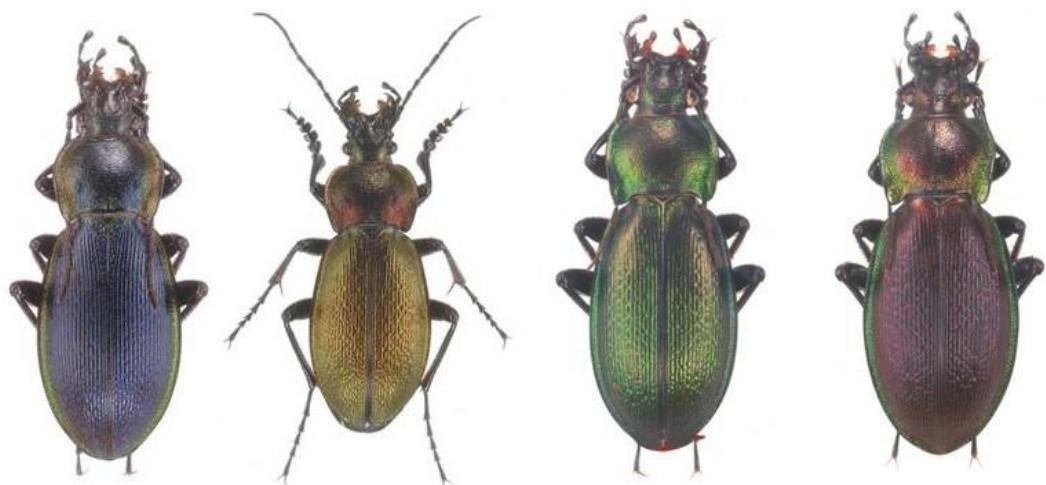
Carabus scheidleri

Carabus scheidleri Panzer, 1799 is a 27-30 mm carabid species with different colours from green through copper to blue. It is a flightless, protected species in Hungary, as are most *Carabus* species (Pictures 2 and 3). Being a generalist predator, this species can be an important natural enemy of aphids and larvae of various insect pests in agricultural areas, small gardens, and parks. The occurrence of this *Carabus* species is demonstrated in Map 2. This ground beetle species is present in some parts of Austria, in Middle- and Southeast-Slovakia (Kleinert 1983), in Southern-Moravia (Pavlíček & Houšková 1989) and in some parts of Hungary (Csiki 1905-1908). It occurs in several types of habitats: *Arrhenatheretea*, *Querco-Fagetea* and agricultural land (Kádár & Szél 1999), fields, meadows and gardens (Pavlíček & Houšková 1989), Austrian potato fields (Kromp 1990), beach forests, hedges, watersides and various types of forests (Korbel 1973), *Quercetum* and *Fagetum* mainly, but it is also common in lowlands and hills (Kleinert 1983). In Hungary this species occurs in the northern and north-eastern mountains, in some southern parts and we can also collect them in some areas of the Great Hungarian Plain. By the results of pitfall trappings in the Pilis Biosphere Reserve *C. scheidleri* is the third most abundant species found in this area, following *Aptinus bombarda* and *Abax parallelepipedus* (Kádár & Szél 1999). In the Pilis Biosphere Reserve the species is associated with disturbed, human-modified areas (Andorkó & Kádár 2006). However, its distribution is well-known, we have sparse information about the biology, population dynamics and the ecology of *C. scheidleri* in Hungary (Andorkó et al. 2005).

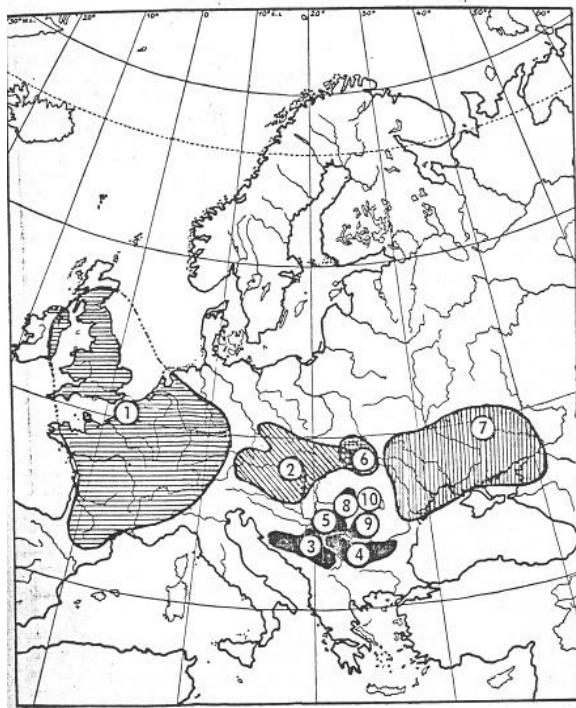


1. *Carabus arvensis*, 2. *obsoletus*, 3. *monilis*, 4. *Scheidleri*, 5. *nemoralis*, 6. *convexus*,
7. *hortensis*, 8. *silvestris*, 9. *Linnei*, 10. *marginalis*, 11. *glabratus*.

Picture 2. *Carabus scheidleri* (drawing 4a on the picture). (E. Reitter: "Fauna Germanica", Band 1 (1908), Table 4.) *Fauna Germanica: Die Käfer des deutschen Reiches* (vol. I, pl. 6). K.G. Lutz' Verlag, Stuttgart.



Picture 3. *Carabus scheidleri* PANZER 1799 var. *jucundus* CSEKI (Photo: I. Retezár)



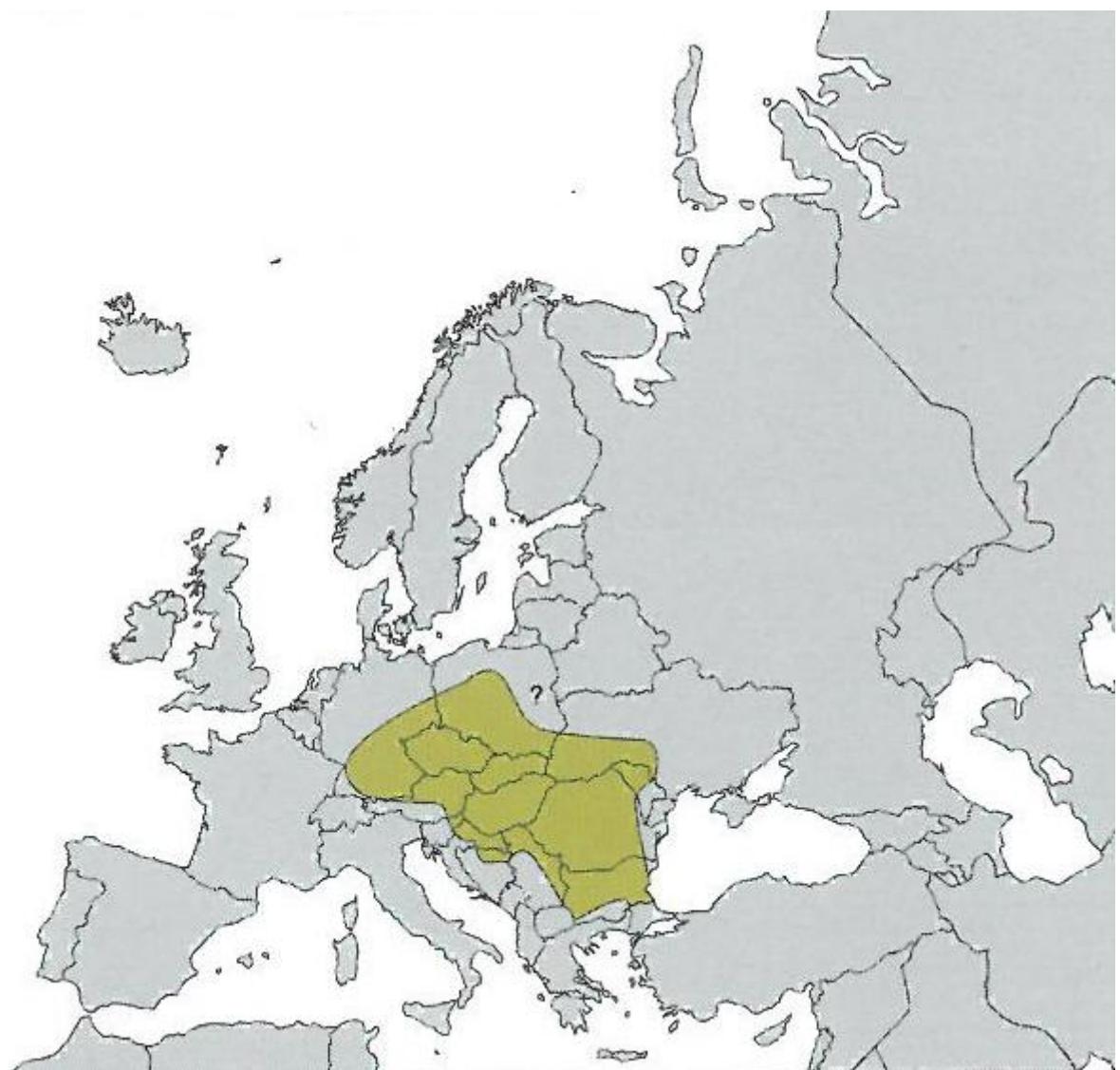
1. *Carabus monilis* Fabricius
2. *Carabus scheidleri* Panzer
3. *Carabus praecellens* Palliardi
4. *Carabus simulator* Kraatz
5. *Carabus kollari* Palliardi
6. *Carabus zawadskii* Kraatz
7. *Carabus excellens* Fabricius
8. *Carabus comptus* Dejean
9. *Carabus rothi* Dejean & Boisduval
10. *Carabus hampei* Küster

Map 2. The distribution of *Carabus scheidleri* and of some closely related species in Europe (Gauckler 1975)

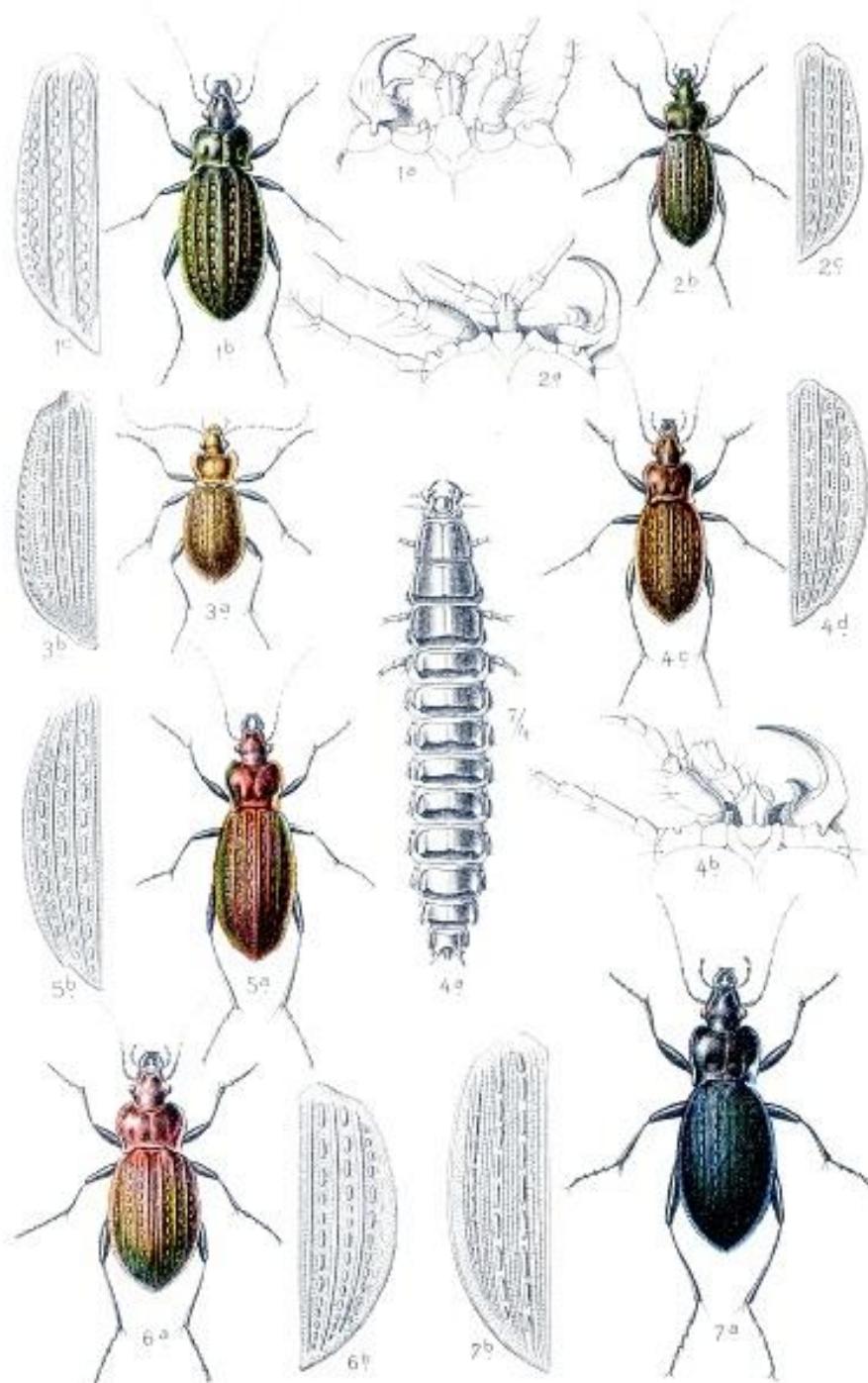
Carabus ullrichi

In the meantime, within the framework of the Man and the Biosphere Programme (MAB) in the course of the long-term monitoring project which was started in the Pilis Biosphere Reserve (PBR), we also studied another large carabid beetle, *Carabus ullrichi* Germar, 1824 (Picture 4). This is an eurytopic species, but it occurs more frequently in hills and forests in Hungary. This species is also widely distributed, but not so common. The conservation status of this species is sparsely estimated in Europe; it is noted on the Red List in Northern Europe as declining or endangered species (Turin et al. 2003; Map 3). Therefore the main population characteristics (i.e. seasonality, reproduction) of this species should be requested for further conservation efforts.

According to Turin et al. (2003) *C. ullrichi* is found in grasslands, gardens, vineyards and from other open habitats to scrub, hedge rows, forest edges and open forests. In Germany this species prefers the deciduous forests, particularly heavy soil types such as loam and limestone, frequently under thermophilic conditions (Arndt 1989). Based on the results of Hürka (1996) this species lives in lowlands and foothills, inhabiting meadows, fields, scrub and open forests. In Hungary it was captured mainly from montane forests associations, but it was also found in the plains, in humid forest meadows and in the hills as well. In Bulgaria this species occurred from lowlands up to 600 m altitude (Guéorguiev & Guéorguiev 1995).



Map 3. The distribution of *Carabus (Eucarabus) ullrichi* in Europe (Turin et al. 2003)



1. *Carabus clathratus*, 2. *granulatus*, 3. var. *interstitialis*, 4. *cancellatus*, 5. var. *emarginatus*,
6. *Ullrichi*, 7. *calenatus*.

Picture 4. *Carabus ullrichi* (drawing 6a on the picture). (E. Reitter: "Fauna Germanica", Band 1 (1908), Table 5.)

3.2.2 Study area and sampling

The reproductive characteristics of *C. scheidleri* were studied in an abandoned, uncultivated field at Nagykovácsi (Julianna-major), in the northwest vicinity of Budapest, Central Hungary (GPS coordinates: N 47°32'47.49", E 18°55'44.43") (Picture 5). The study area was bordered by an oak forest (*Quercetum petreeae-cerris*), an abandoned apple orchard on a hillside, shrubs, grassy areas near the forest edge, and a mosaic of cultivated fields (alfalfa, winter wheat, small vegetable gardens). The surface of the basin is covered by loess, under this layer older waterproof rocks – like sandstone and clay – are situated. All around this basin sod-slopes with limestone are found. The examined plot was an uncultivated field (1 ha) abandoned for more than ten years, where the vegetation contained *Solidago* sp., *Arrhenatherum elatius*, *Agropyron repens*, *Melilotus officinalis*, *Campanula glomerata*, *Carlina vulgaris*, *Picris hieracioides*, and several shrubs, mainly *Rosa* sp.

Ten pitfall traps (plastic jars of 80 mm diameter, containing 4% formaldehyde as a killing and preserving agent) were installed in two rows. The rows were 10 meters apart and the distance between the traps was 5 meters.

Samples were collected weekly between mid-May and the end of August in 2000 and 2001. Due to the fact that individuals were already found in mid-May, in 2002 we started sampling at the end of April and it lasted until mid-September. Due to the improper sampling storage, data gained from 2000 cannot be used for further statistical analyses, however the global trend in these data are mentioned in the proper context in the results section.

Collections were sieved and transferred to 4% formaldehyde in the field, sorted under microscope in the laboratory and stored in the same fluid for dissection.



Picture 5. Early spring view of the study area of *Carabus scheidleri* (Julianna-major, Budapest-Nagykovácsi). The arrow indicates the location of the sampling. (Photo: R. Andorkó)

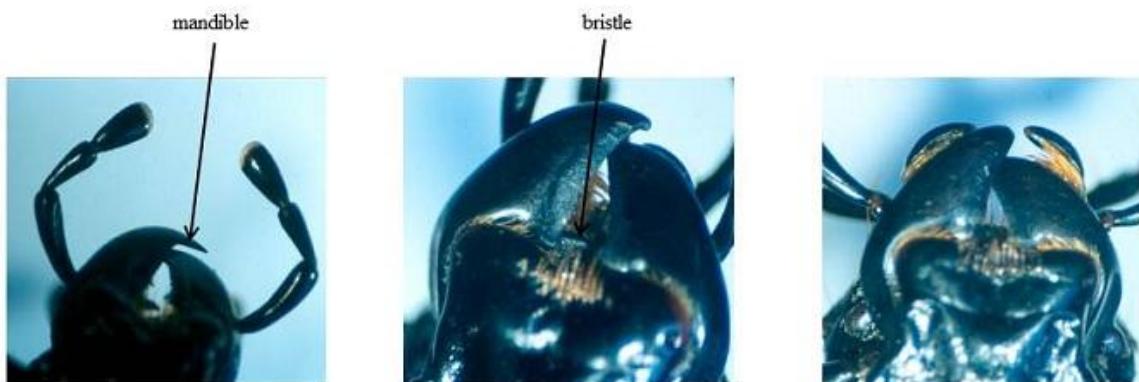
In case of *C. ullrichi* the individuals were captured from the same area (PBR) as already described in the first section of this thesis. Beetles were collected in 2005 and in 2006 from the end of April until the end of September. To explain the possible effects of environmental differences among the three studied habitats at PBR, we measured the most relevant environmental variables, which could have an influence on the distribution of the carabids (Butterfield et al. 1995): relative air humidity, light intensity, ground and air temperature. These variables were measured in a five-meter radius around the pitfall traps in each habitat every sampling occasion in every season.

3.2.3 Age determination

Beetles from each sample were sexed, aged and dissected to assess reproductive status. Dissection was carried out under exhausting the formaldehyde atmosphere. Ageing was firstly

based on the size of bristles and on mandible wear, elytral hardness and coloration (van Dijk 1972, 1979):

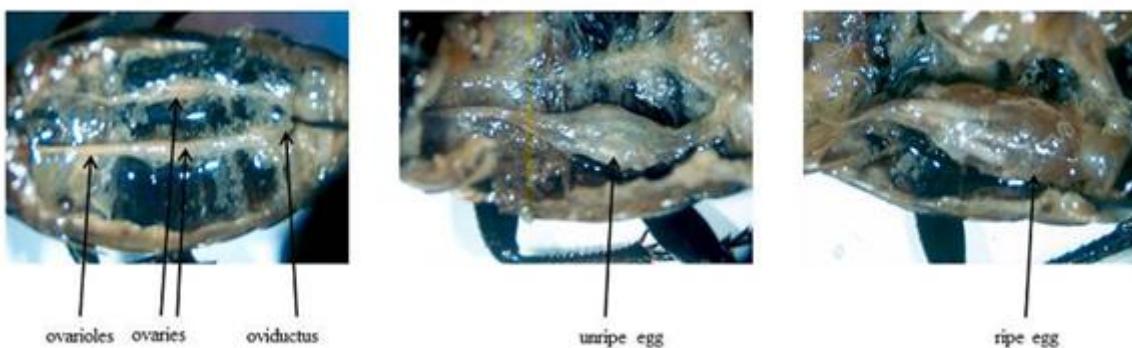
1. young beetles: soft or flexible elytra, sharp, unworn mandibles, long and intact bristles, representing the new generation adults and individuals from the overwintered cohort in their first breeding season;
2. old beetles: hard and fully coloured elytra, severely worn mandibles and bristles, found in beetles in their second or third breeding season. Many of these beetles were probably approaching the end of their lives;
3. middle-aged beetles: transition between the two categories, with hardened sclerite, little wear on the mandibles and on the bristles.



Pictures 6, 7 and 8 (from left to right). Ageing based on the length and extent of bristles and on mandible wear. Young beetles: sharp mandibles (6); middle-aged beetles: transition between the two categories, with little wear on the mandibles (7); old beetles: severely worn mandibles and few bristles (8). (Photos: R. Andorkó)

Females were dissected in order to determine the developmental stage of their ovaries and the number of eggs found in their ovaries, following the method of van Dijk (1972, 1979), Wallin (1989) and Diefenbach et al. (1991). Three categories were distinguished:

- (a) immature beetles without eggs in ovaries, having compact, long ovaries, lateral oviducts which are narrow and twice as long as the common oviduct (prereproductive stage) (Picture 9);
- (b) gravid beetles with eggs of different stages of maturation present in the ovaries, and the lateral oviducts have wider diameter (reproductive stage) (Pictures 10 and 11);
- (c) spent beetles with large lateral oviducts; ovaries less compact than those of an immature female. Such beetles passed at least one reproductive season (postreproductive stage).



Pictures 9, 10 and 11 (from left to right). Dorsal view of *Carabus scheidleri*'s abdomen with the dorsal tergites removed. Immature beetles without eggs in the ovaries (9); ovaries with unripe eggs, and visible ovarioles (10); gravid beetle with one ripe egg (11). (Photos: R. Andorkó)

3.2.4 Data analysis

The repeated measures ANOVA was used to test for differences based on the total number of individuals, the total number of females and males per trap between the years. This test was also used to test for differences between the mean abundances of females and males per trap according to their age and ovary categories (in females only). Significant difference among the sampling periods was revealed by Fisher's *post hoc* LSD test. The normal distribution of the dataset was tested by Shapiro-Wilk test. According to the results of this test we transformed the data logarithmically ($\log(x+1)$). The Statistica 6.0 program was used for

analysis (Statsoft 2000). The species counts were standardised for trapping days, furthermore these data were converted into fortnights.

3.2.5 Species-habitat modelling

We used the general analytical approach (based on Franklin et al. 2000) already described in part 2.2.2 in order to study the main effects of habitat selection of *C. ullrichi*. We formed *a priori* verbal hypotheses, which we then expressed as models that could be fit to the available data. In these models, the response variable was species abundance per habitat type. The explanatory variables were the studied ecological and environmental factors as fix effects. During the species-habitat modelling we used generalised linear models to explore the impacts of the habitat type and quality for the distribution of the studied species. Before the modelling, the possible dependencies among the (potential) variables were checked using Spearman rank correlation or non-parametric Kruskal-Wallis analysis of variance. We used the following variables in the evaluation of models: habitat-type (beech, transition zone, oak); relative humidity, light intensity, ground and air temperature.

3.2.6 ‘Seasonality models’

We used the same above mentioned approach in part of 2.2.2 in order to study the main effects of seasonality on life-history characteristics of the studied species. Based on the above mentioned protocol we defined *a priori* models. In the models the abundance according to gender, the age composition, the stages of the ovaries and the number of eggs were the response variables. Effects of habitat type, seasonality and year on the dependent variables were tested in the models.

3.3 Results

3.3.1 General results

In relation to the examination of *C. scheidleri* we captured 959 individuals, 591 females and 368 males during the three consecutive years of 2000-2002 (Table 6).

Based on the three-year-sampling period experiences the activity period of *C. scheidleri* lasted from the beginning of May until the beginning of September, with two activity peaks in the first two years and with one in 2002. In 2000 the activity peaks occurred at the end of June and at the end of July. In 2001 the main activity period occurred from mid-May until mid-July, however there were two activity peaks at the beginning of the season, one in mid-May and the other at the beginning of July. The late activity period occurred from the end of July until the end of the trapping season. In 2002 the main activity period occurred between the end of June and the beginning of August. The activity peak was at the end of July. The seasonal dynamics curve was skewed to the right in 2002 (Figure 11).

In all years there were more females captured than males, however, the seasonal activity of both sexes was similar in each year. In 2000 only a slightly higher number of females were caught. In 2001 there were three times more, whereas in 2002 only twice as many females than males in the traps. The mean number of males showed significant difference between 2001 and 2002 [$F(1; 63) = 4.25$; $p = 0.04$]. The mean number of females did not differ significantly between 2001 and 2002 [$F(1; 63) = 0.01$; $p = 0.9$].

Table 6. Characteristics of the *Carabus scheidleri* population investigated at Nagykovácsi, Central Hungary in 2000, 2001 and 2002.

	2000	2001	2002
Total catch (females/males)	342(174/168)	237(172/65)	380(245/135)
No. of females per age class (young/middle-aged/old)	78/45/51	146/17/9	171/56/18
No. of males per age class (young/middle-aged/old)	86/41/41	61/4/0	80/29/26
No. of females per reproductive class (immature/gravid/spent)	20/98/56	38/122/12	48/163/34
Total no. of ripe eggs found	1029	802	1311
Mean number of ripe eggs per female (SD)	5.91 ± 5.38	4.66 ± 4.24	5.35 ± 5.13

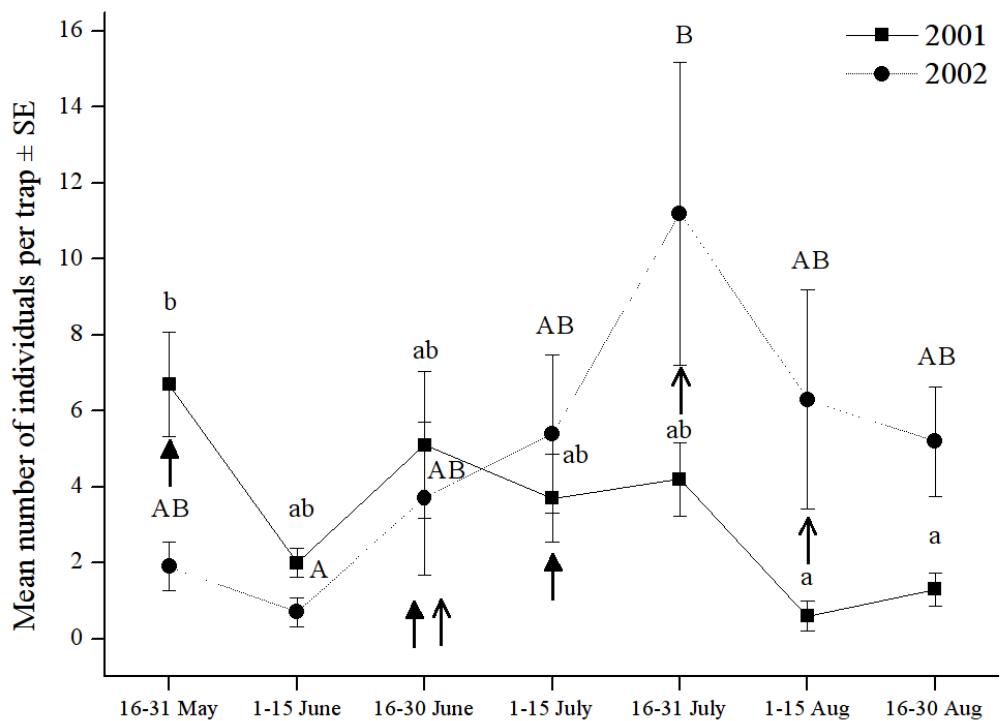


Figure 11. Seasonal activity of *Carabus scheidleri* individuals at Nagykovácsi, Central Hungary in 2001 and in 2002. The arrows denote the main activity period (left and right arrows) and activity peaks (middle arrows) (filled arrows: 2001, regular arrows: 2002). (Different letters indicate significant ($p < 0.05$) differences within the given year by Fisher's post-hoc LSD test.) Repeated measures ANOVA between the years: $[F (1; 63) = 0.67; p = 0.41]$.

A total of 895 *C. ullrichi* individuals were captured, 498 females and 397 males during the two consecutive years (Table 7). The activity period of the two years of sampling lasted from the end of April until the end of September with two activity peaks (Figure 12). This activity period mostly covered the entire activity period, because very low number of individuals was captured in the area in the first sampling occasion and in the course of the latest sampling occasion. In 2005, the first slight activity peak in all three habitats occurred at the end of May and the second peak was at the end of August. The main activity period was from the end of May until the beginning of July. The early activity period occurred from the beginning of the trapping until the end of May, and the late activity period occurred during August. The seasonal activity curve was strongly skewed to the left. The activity profile was similar in 2006 as well. The number of the females was mostly similar to the number of the males, and their activity peaks were also similar.

Table 7. Characteristics of *Carabus ullrichi* population investigated in the Pilis Biosphere Reserve, in 2005 and 2006.

	2005			2006		
	<i>beech</i>	<i>transition</i>	<i>oak</i>	<i>beech</i>	<i>transition</i>	<i>oak</i>
Total catch (females/males)	94 (58/36)	88 (50/38)	154 (73/81)	167 (95/72)	129 (86/43)	263 (136/127)
No. of females per age class (young/middle-aged/old)	55/3/0	46/3/1	70/0/2	89/5/1	83/2/1	134/1/1
No. of males per age class (young/middle-aged/old)	34/1/1	36/1/1	78/2/1	70/1/1	43/0/0	119/4/4
No. of females per reproductive class (immature/gravid/spent)	21/35/2	17/28/5	49/23/1	60/27/8	46/34/6	91/42/3
Total no. of ripe eggs found	58	50	73	95	86	136
Mean number of ripe eggs per female (SD)	1.08±1.67	1.12±1.88	0.52±1.60	0.65±1.38	0.70±1.29	0.50±1.17

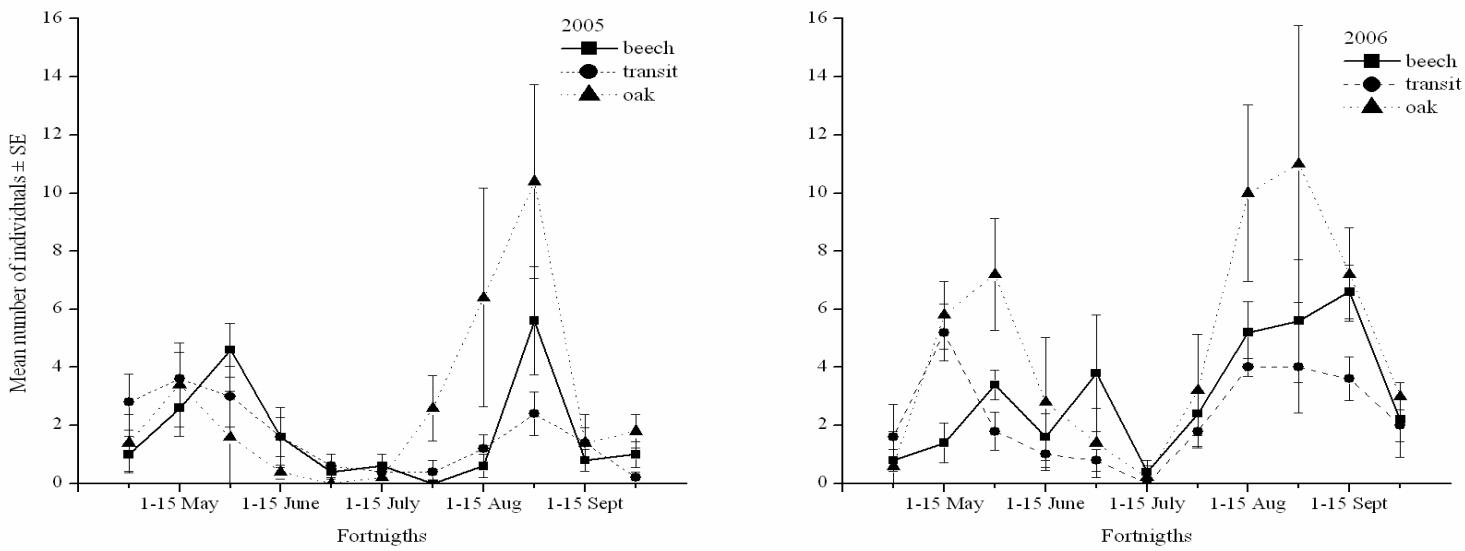


Figure 12. Seasonal activity of *Carabus ullrichi* individuals in the three habitats in the Pilis Biosphere Reserve, in 2005 and 2006.

3.3.2 Age composition based on mandible wear

Carabus scheidleri

In case of *C. scheidleri* in 2000 young, middle-aged and old males were caught during the whole season, and the young adults dominated. In 2001 almost only young males were found (Figure 13). In 2002 we captured young males during the whole season, middle-aged males in lower numbers almost during the whole season, and old beetles in July in high numbers.

All three age categories of *C. scheidleri* females were found in each year. In 2000, the numbers of the females of different age-categories were very similar, but young beetles dominated. In 2001, we captured nearly exclusively young females, but we also found some middle-aged individuals in the middle of the season and some old individuals during the whole season (Figure 14). In 2002, young females dominated, and we caught middle-aged and old females from the middle to the end of the season.

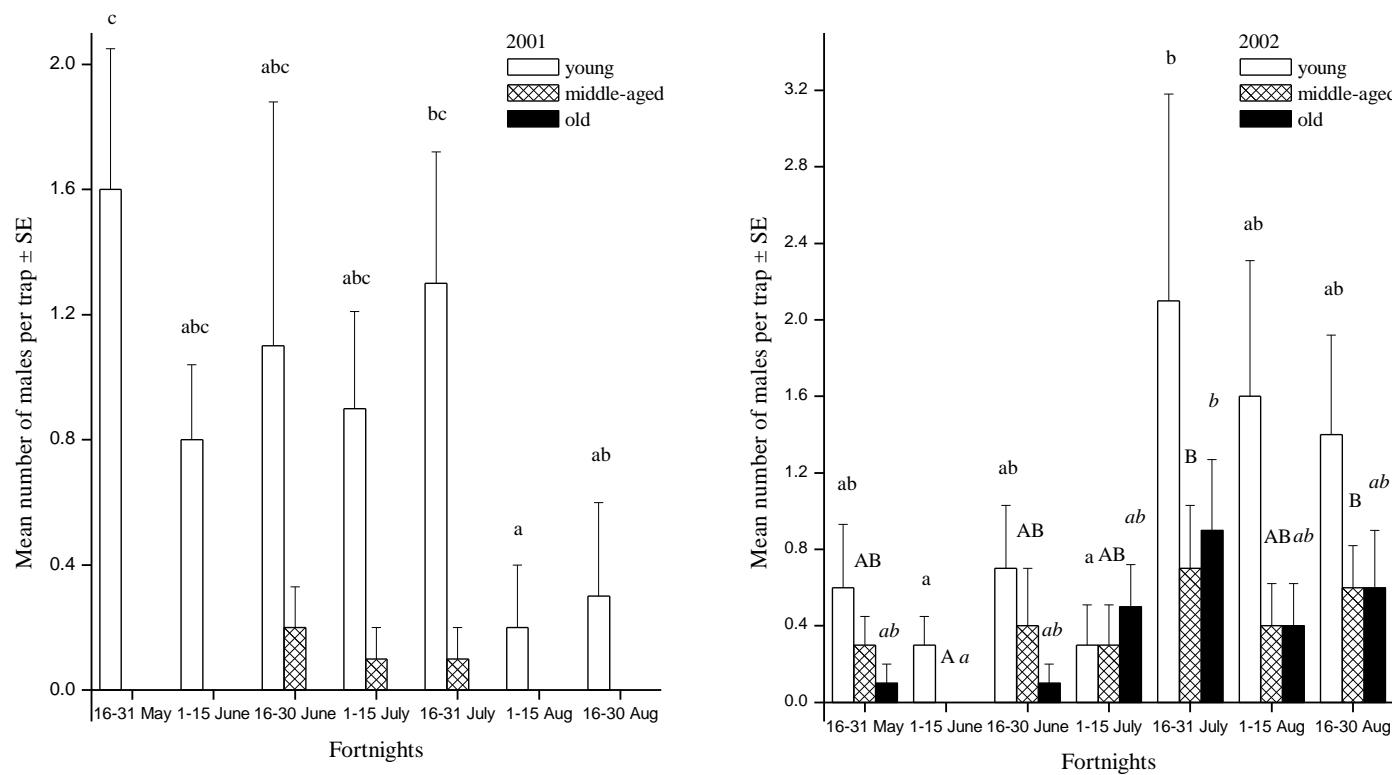


Figure 13. Different age-categories based on mandible wear of *Carabus scheidleri* males collected by pitfall traps at Nagykovácsi, Central Hungary in 2001 and in 2002. (Different letters indicate significant ($p<0.05$) differences within the age-categories by Fisher's *post-hoc* LSD test.) Repeated measures ANOVA between the years: young: $[F(1; 63) = 0.0009; p = 0.97]$; middle-aged: $[F(1; 63) = 14.45; p < 0.001]$; old: there were no old males in 2001.

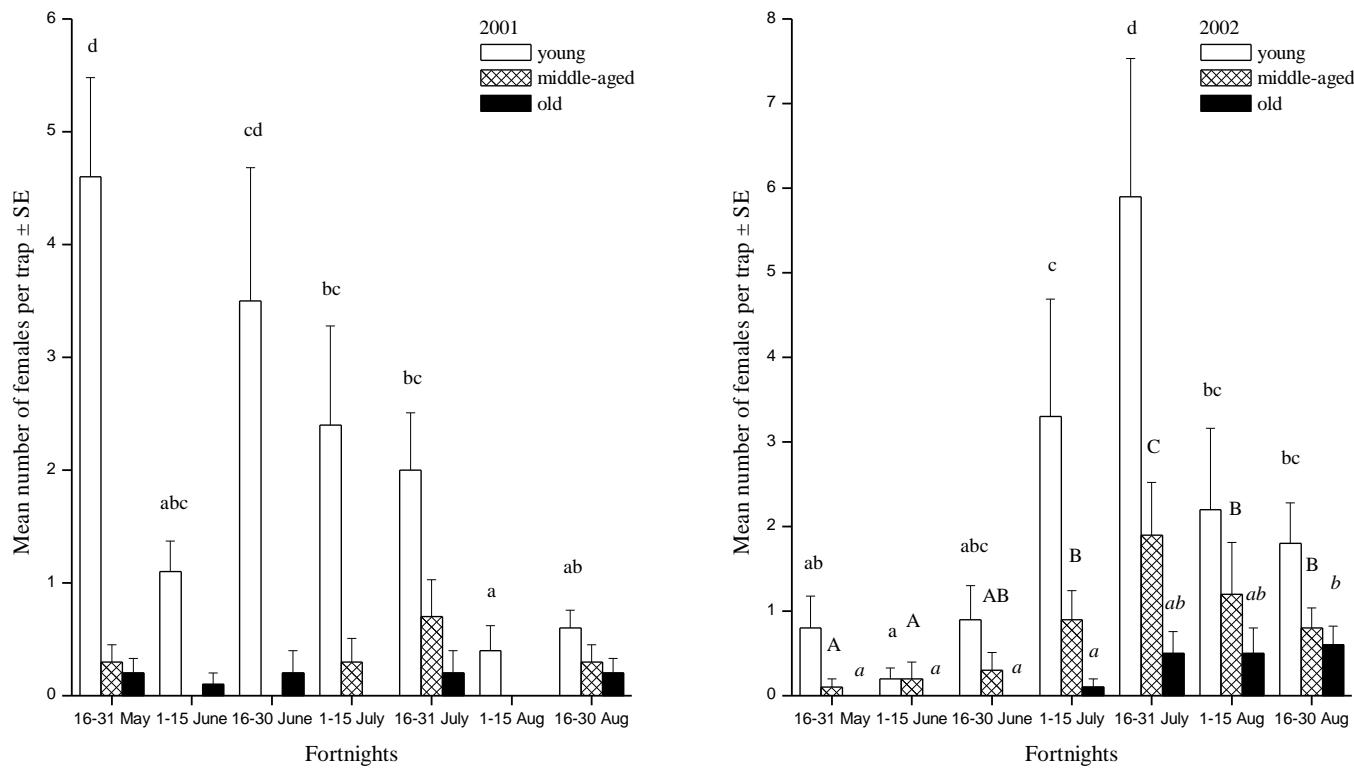


Figure 14.: Different age-categories of *Carabus scheidleri* females collected by pitfall traps at Nagykovácsi, Central Hungary in 2001 and in 2002. (Different letters indicate significant ($p<0.05$) differences within the age-categories by Fisher's *post-hoc* LSD test.) Repeated measures ANOVA between the years: young: $[F(1; 63) = 0.46; p = 0.49]$; middle-aged: $[F(1; 63) = 9.67; p < 0.01]$; old: $[F(1; 63) = 2.15; p = 0.14]$.

Carabus ullrichi

In case of *C. ullrichi* in both years (in 2005 and 2006) – based on the age estimation of the mandible wear –, the young females and males dominated (Figures 15 and 16). Only a few middle-aged and old beetles were found in the three habitats. The highest number of the young males was captured at the beginning of August. The abundance of young males showed particular difference among the habitat types suggesting high activity density in the oak forest.

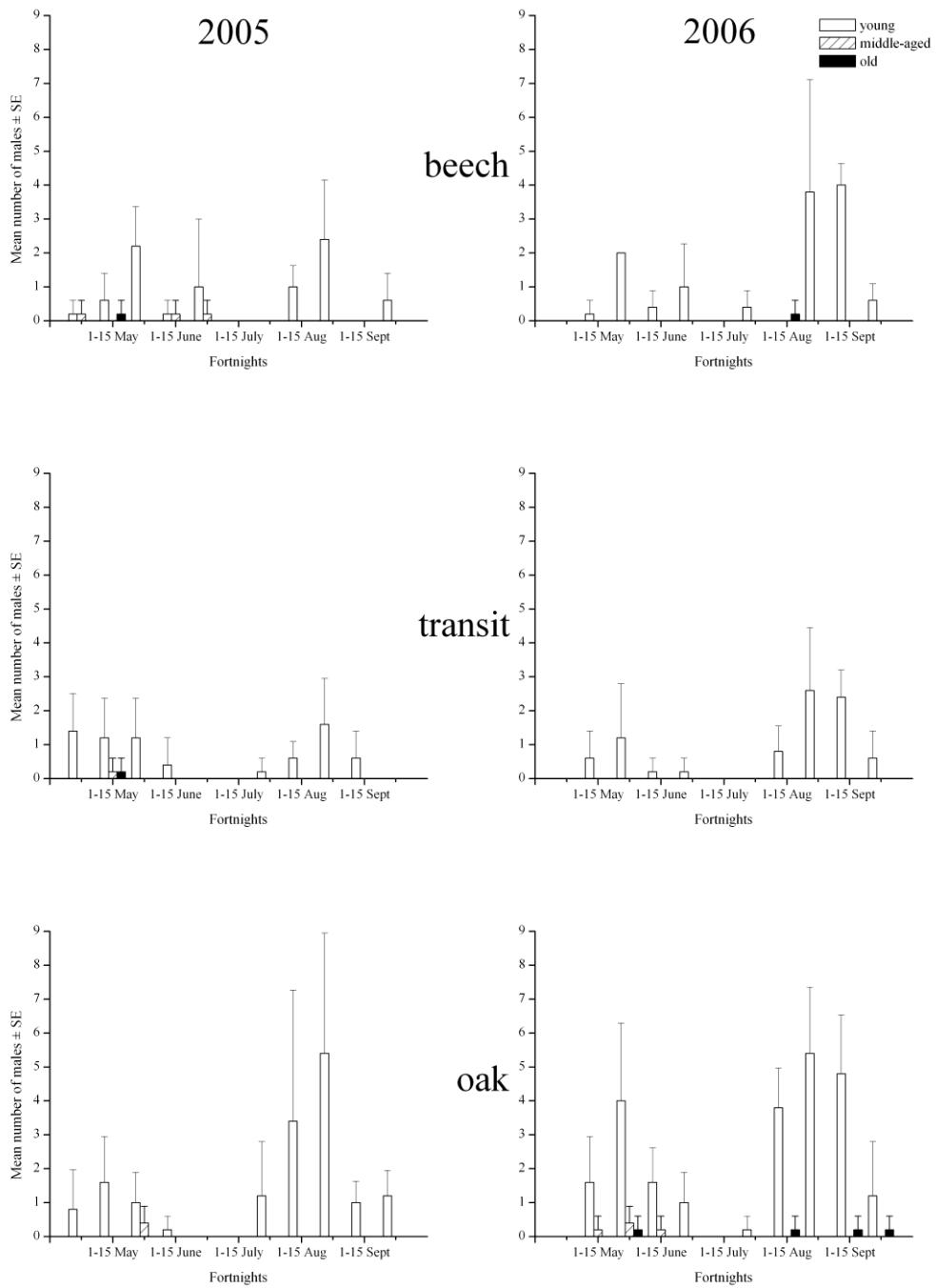


Figure 15. Different age-categories determined by mandible wear of *Carabus ullrichi* males in the three habitats in the Pilis Biosphere Reserve, in 2005 and 2006.

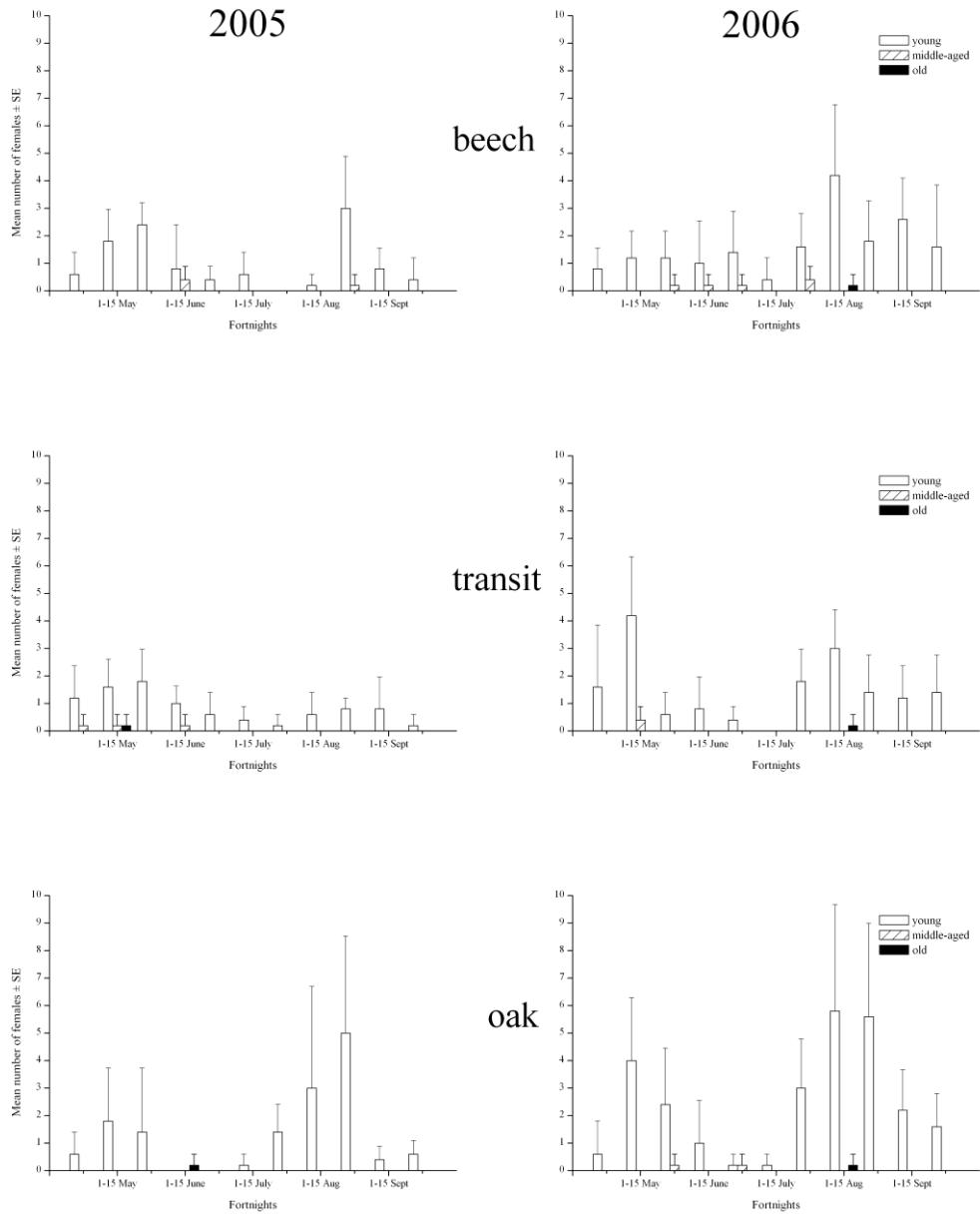


Figure 16. Different age-categories determined by mandible wear of *Carabus ullrichi* females in the three habitats in the Pilis Biosphere Reserve, in 2005 and 2006.

3.3.3 Reproductive characteristics of females based on the examination of ovaries

Carabus scheidleri

According to the results from the dissection of the *C. scheidleri* females, we found immature beetles in every year. In 2000, we found few immature individuals. In 2001, the peak of the immature females was at the end of May (Figure 17), and in 2002 we caught more immature females in the middle of the season. In 2000, the peak of gravid females occurred at the end of June, in 2001 the peaks occurred at the end of May and at the end of June, and in 2002 one peak occurred at the end of July. A high number of spent females were found in 2000 with one peak at the beginning of July. In 2001, we caught just some of these females. And in 2002 we captured some spent females at the end of the season.

Carabus ullrichi

According to the results from the dissection of the *C. ullrichi* females (Figure 18), we found immature beetles in every year. In 2005, in all habitats the peak of the immature females occurred at the end of August and that of the mature females was at the end of May. We found only some of the spent females at the beginning of the season. During the following year we captured the most immature females in all habitats at the beginning of August and that of the mature females at the beginning of May. Few spent females were also present in the samples during the whole season. The abundance of females with immature ovaries was the highest in the oak forest (Table 8). The number of ripe eggs found in the ovaries is given in Table 7.

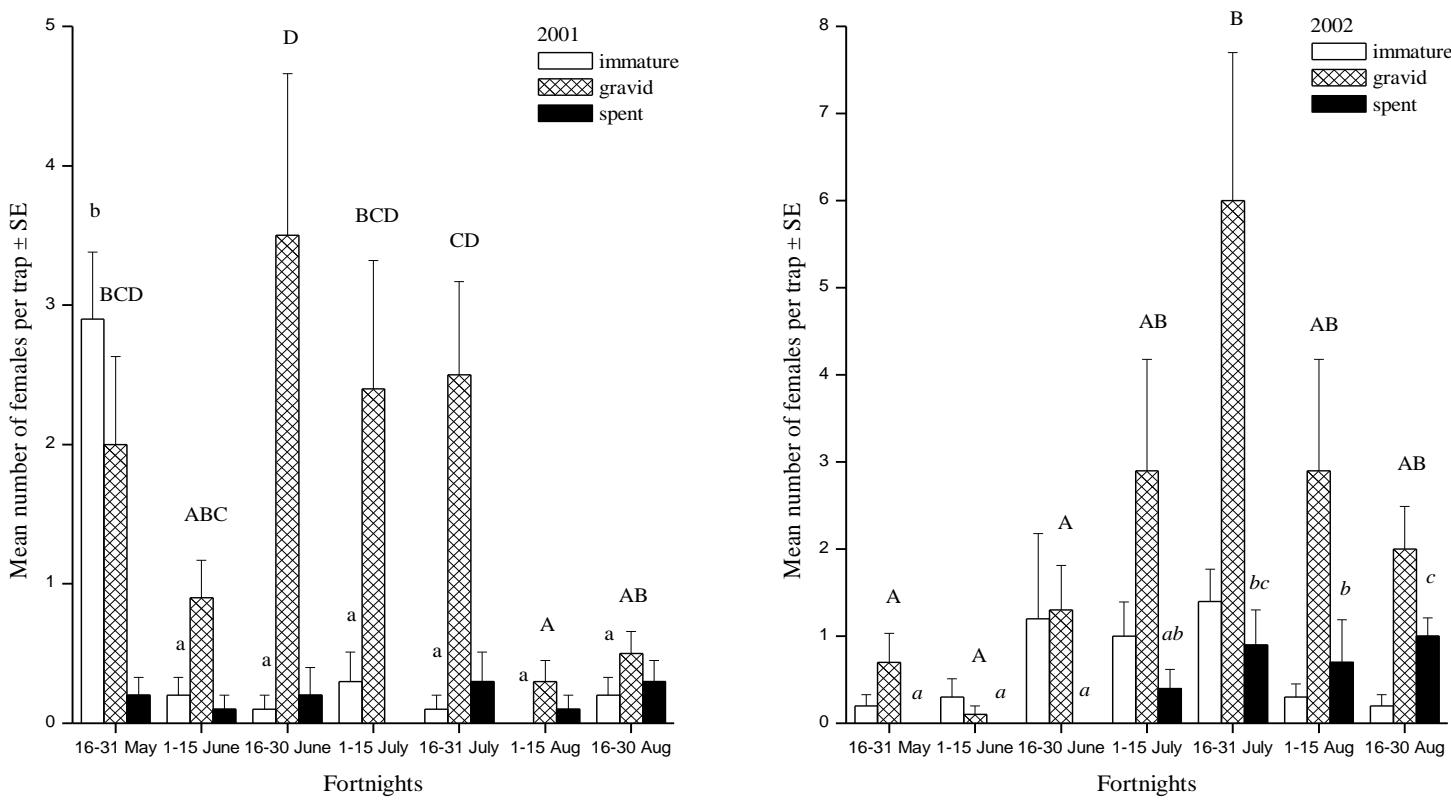


Figure 17. The mean number of *C. scheidleri* females in their respective reproductive stages captured by pitfall traps at Nagykovácsi, Central Hungary in 2001 and in 2002. (Different letters indicate significant ($p < 0.05$) differences within the respective reproductive stages by Fisher's *post-hoc* LSD test.) Repeated measures ANOVA between the years: immature: $[F (1; 63) = 0.82; p = 0.36]$; gravid: $[F (1; 63) = 0.35; p = 0.55]$; spent: $[F (1; 63) = 5.47; p = 0.02]$.

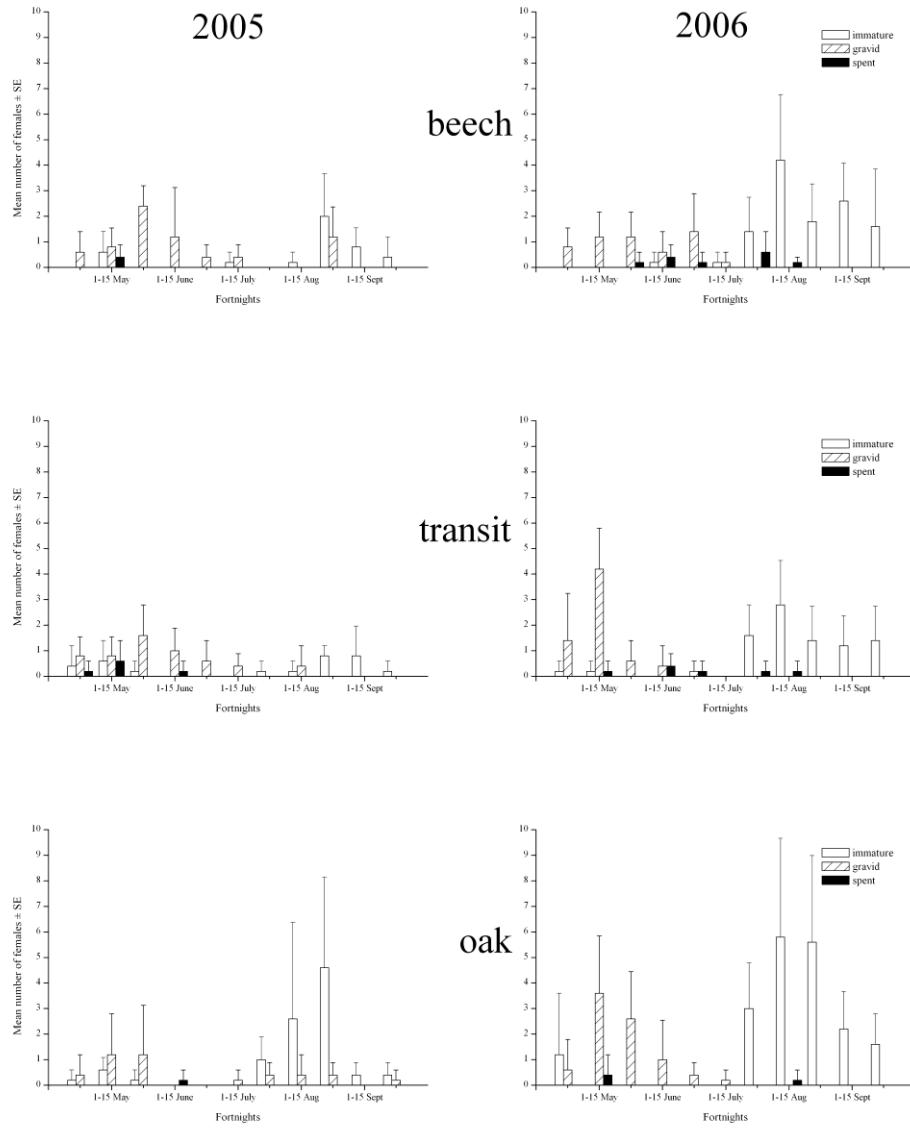


Figure 18. The mean number of *Carabus ullrichi* females in their respective reproductive stages in the three habitats in the Pilis Biosphere Reserve, in 2005 and 2006.

3.3.4 Number of ripe eggs found in the ovaries

Whereas the inspection of the developmental stages of ovaries gave an overall picture about the actual reproductive status of females, the number of ripe eggs in the ovaries could shed light on at least one, and possibly more past reproductive events. The number of ripe eggs found in the ovaries of *C. scheidleri* is given in Table 6. We found consistent patterns between the activity of females and the number of ripe eggs according to sampling dates. Ripe eggs were found in the ovaries from the end of May until the end of August.

The mean number of ripe eggs in *C. scheidleri* was 5.91 in 2000, 4.66 in 2001 and 5.35 in 2002 (Table 6). There was no significant difference in the population's mean egg number between years 2001 and 2002 [$F(1; 63) = 0.24$; $p = 0.62$]. Females had a maximum of 22 ripe eggs. The most frequent egg number during the three years was two.

C. ullrichi females had a maximum of seven ripe eggs per individual. The most frequent egg number during the two years was two. The number of ripe eggs found in the ovaries did not show significant differences among the habitats (Table 7). The mean number of ripe eggs per female was 0.9 in 2005 and 0.65 in 2006. The number of the maximum ripe eggs per gravid female was 1.82 in 2005 and 1.85 in 2006.

3.3.5 Species - habitat and seasonality modelling

This assessment was only applied to *C. ullrichi* as it was already mentioned above. The results of the species-habitat modelling showed that the light intensity model fitted best for *C. ullrichi* (Table 8), occurring in the highest number in the oak forest. We found significant differences in habitat selection according to the overall abundance, the young male, and also the immature models. Therefore, these patterns were revealed by the results of seasonality models (Table 9). We found no significant difference in the abundance between the years, but there were significant differences among the sampling periods.

Table 8. Age and reproductive phase distribution of *Carabus ulrichi* by two kinds of model in the Pilis Biosphere Reserve, in 2005 and 2006. Model selection was based on Akaike Information Criteria (Akaike 1974). In the columns the average predicted values (beta) indicated as the descriptor of the magnitude of the effect.

Average predicted values with S.D.				
model's name	beech	transition	oak	comparison
<i>species-habitat models</i>				
light-intensity model	3.94±0.22	3.76±0.17	4.39±0.08	O>B**; O>T***
<i>seasonality models</i>				
1-overall abundance	0.9±0.5	0.85±0.5	1.15±0.5	O>B**; O>T**
2-young-male	0.44±0.38	0.38±0.38	0.73±0.38	O>B***; O>T***
3-middle-aged-male	0.01±0.02	0.006±0.02	0.03±0.02	NS
4-old-male	0.01±0.01	0.006±0.01	0.02±0.01	NS
5-young-female	0.63±0.33	0.58±0.33	0.72±0.33	NS
6-middle-aged-female	0.05±0.03	0.03±0.03	0.01±0.03	NS
7-old-female	0.006±0.02	0.01±0.02	0.01±0.02	NS
8-immature	0.34±0.38	0.29±0.38	0.48±0.38	O>T**
9-gravid	0.3±0.28	0.28±0.28	0.27±0.28	NS
10-spent	0.06±0.05	0.06±0.05	0.02±0.05	NS
11-eggs	0.4±0.43	0.37±0.43	0.29±0.43	NS

* p<0.05; ** p<0.01; *** p<0.001. Beech, B= beech forest; transition, T= transition zone; oak, O= oak forest.

Table 9. Distribution by age and reproductive stage of the population size of *Carabus ullrichi* over the sampling period in three habitat types (beech, transition zone and oak) in the Pilis Biosphere Reserve, in 2005 and 2006. The numbers in the lines designated as “estimated” give the deviation of increase or decrease of adult beetles’ population size of all habitats combined from the expected value. The asterisks sign significant differences in comparison with the own expected value within a given time interval. Model selection was based on Akaike Information Criteria (Akaike 1974).

model name	Fortnights										
	16-30 April	1-15 May	16-30 May	1-15 June	16-30 June	1-15 July	16-30 July	1-15 Aug	16-30 Aug	1-15 Sept	16-30 Sept
overall abundance											
estimated	-0.77	-0.009	-0.01	-0.68	-0.91	-1.19	-0.61	1.12	0.37	-0.15	-0.6
error	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.13	0.16	0.16	0.16
p	***	ns	ns	***	***	***	***	***	*	ns	***
young-male											
estimated	-0.49	-0.19	0.19	-0.41	-0.45	-0.71	-0.53	0.56	0.59	0.2	-0.31
error	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.1	0.13	0.13	0.13
p	***	ns	ns	**	***	***	***	***	***	ns	*
immature											
estimated	-0.82	-0.69	-0.86	-0.88	-0.9	-0.86	-0.32	0.75	0.16	-0.23	-0.42
error	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.09	0.12	0.12	0.12
p	***	***	***	***	***	***	**	***	ns	ns	***

* p<0.05; ** p<0.01; *** p<0.001.

3.4 Discussion

The determination of the mandible wear proved to be the most precise method for age-estimation (Fazekas 1997). According to Sparks et al. (1995) this ageing can be used for illustration only and not for age-estimation. Based on our experiences the determination of the mandible wear for age-estimation could be an objective estimation, which is sex- and size-independent. In the case of *C. scheidleri*, we could estimate the age of the adults and also the type of overwintering, which were supported by the results of the dissection. Accordingly (Andorkó et al. 2007), mandible wear is a good age estimator when different generations of the species do not overlap, like in case of *C. ullrichi*. When generations overlap, the two age-estimations - the one based on mandible wear and the other on the developmental stage of the ovaries - together give good results. Therefore, if the age estimation based on mandible wear is supported by the results of the dissection, it could be a particularly precise method (Andorkó et al. 2005). According to the results of Spearman rank correlation (Andorkó et al. 2007) in case of *C. ullrichi* the two age-estimations provided clearly separated age-classes. The opposite result was found in case of *C. scheidleri*, where the age-classes were overlapped (Andorkó et al. 2007). Because of the absence of middle-aged and old *C. scheidleri* males in the activity in 2001, we suppose that males live for just one year. In carabid beetles it is well-known that in general females live longer than males (Kreckwitz 1970; Hůrka 1973). Females live longer also in this case.

3.4.1 *Carabus scheidleri*

We summarize that *C. scheidleri* develops during one year, overwinters both as larva and as adult, adult females live more than one year, they reproduce more than once, and the different generations overlap during one season, assuring the persistence of the population. Old beetles participate also in the reproduction.

Young and immature *C. scheidleri* females appearing at the beginning of the season overwintered probably as adults, and this will be their first reproductive period (Figure 11). Mature females appearing at the beginning of the season overwintered also as adults, but this will be their second reproductive period. The spent females have already reproduced. It means that most females probably live for two years. The presence of immature females in the middle and at the end of the season would indicate that a portion of the population also

overwinters as larvae (Figure 17, Table 6). The activity peaks are similar to the reproductive peaks in the case of *C. scheidleri*, therefore the reproductive period overlaps with the activity period. This is not obvious in all ground beetles, for example the reproductive peak occurred earlier than the activity peak in the case of *Anisodactylus signatus* in Hungary (Fazekas et al. 1997). In case of *Pterostichus melanarius* the seasonal dynamics of activity is characterized by two peaks (in mid-June-early July and in late July-mid-August); both hibernated immature adults and adults that had already bred before wintering start reproduction simultaneously (Matalin 2006).

In the case of *C. scheidleri* more gravid females (that may reproduce) were found in the season, than in other *Carabus* species, for example in *C. convexus*, *C. hortensis*, *C. violaceus*, *C. coriaceus* (Fazekas 1997). The presence of old beetles that reproduce increases the chances of the population's survival. The elongation of reproductive period of *C. scheidleri* in the season is similar to those of *Pterostichus melas* and *Harpalus atratus* (Thiele 1977). Since *C. scheidleri* has several reproductive periods in the same season, this phenomenon can also ensure the population's survival. This strategy ensures the persistence of the population at different levels and in different ways.

In general, the high percentage of adults in the old age class suggested that the larger species of the tribe Pterostichini could live longer than one year, and that females could have two or more reproductive periods (Lövei 2008). This has been shown for several other carabid species (Schjøtz-Christensen 1965; van Dijk 1972; Gergely & Lövei 1987; Sota 1984), and is probably much more common in ground beetles than has been previously thought (Lövei & Sunderland 1996).

We tried to classify *C. scheidleri* according to the already known categorisation (Thiele 1977) based on annual rhythm and reproductive characteristics. *C. scheidleri* is a large, nocturnal species, which is unable to fly. This species can overwinter as adult and also as larva. *C. scheidleri* might belong to the species group which Thiele (1977) characterized with having flexible reproductive periods. In such species spring and autumn reproduction can occur side by side in the same population, and what is more important that the larvae may also develop under summer or appropriate winter conditions. The reproductive period may occur at very different periods of the year depending on the climate and the weather.

Based on our results, we suggest this species has evolved to persist in unstable environments and it is well adapted to the human disturbances by its long activity period, by several reproductive periods (high number of ripe eggs in ovaries, the presence of old beetles in the reproduction), by the ability of overwintering both as larvae and adults which can lead to overlapping generations. These generations could cause a relatively high number of individuals as compared to other *Carabus* species, such as *C. nemoralis* and *C. convexus* (Fazekas 1997; Thiele 1977). This might also lead to density dependent competitive success.

According to Matalin (2006) the life-cycle of *Pterostichus melanarius* combines the one-year development with hibernating larvae with two-year development with the hibernating immature and postgenerative adults. He investigated two subpopulation groups, wintering at different phases of the ontogenesis, which were totally isolated at the northern border of the range. Within each subpopulation, individuals were characterized by the biennial life-cycle; and according to the results, the above mentioned polyvariant character of the life-cycle turned into the monovariant one. Such a life-cycle should be designated as the compensatory monovariant cycle, and populations, in which it is realized, as side by side populations. We suggest that the life-cycle of *C. scheidleri* should also be classified as the compensatory monovariant cycle comparing to that of *P. melanarius*.

The above mentioned features might result in that this species can buffer the environmental stochasticity and provide a constant seasonality in terms of less spatio-temporal variation in population size. Large species are often long-lived, have low densities and probably low reproductive capacity which dampens their year-to-year population fluctuations (Luff 1982; Lövei & Sunderland 1996). While these attributes could serve as a spreading the risk strategy, they could make this species also sensitive, because its potential to respond to (unfavourable) environmental variation may be diminished by the accelerated habitat fragmentation/alteration within its distribution area.

3.4.2 *Carabus ullrichi*

Our results confirmed that *C. ullrichi* is a typical spring breeder species with summer larvae (Turin et al. 2003). This species has one reproductive period in the season exclusively and hibernates as adults. This species is a typical forest species (Turin et al. 2003).

C. ullrichi summer larvae were followed by immature females in August which was indicated by the second peak in the activity (Figure 12). The number of mature females showed the reproductive peak in early summer (Figure 18). Afterwards, the small number of individuals indicated that the beetles had died off after the reproductive period and we found only a few number of spent females. There were no eggs in those individuals. We suggest that the first activity peak overlaps with the reproductive peak which occurs in May. The other activity peak occurs in August when the beetles do not reproduce. Based on these traits we suggest that *C. ullrichi* beetles reproduce only once during one season in their life-time in forested habitats in Hungary. Our suggestion is also confirmed by the results of Burmeister (1939) and Verhoeff (1917) obtained in the Little Carpathian on the ridge Veterlín hill, at an altitude range of 500 – 723.5 m in oak and beech forests.

The results of species-habitat modelling (Table 8) showed that *C. ullrichi* selects the habitats according to the light intensity. Thus, it occurred in the highest number in the more opened oak forest, but the species could use all the habitat types simultaneously. However, we captured more individuals in the oak forest than in the other habitat types. There were no differences either in the seasonal activity patterns, or in the age-composition, or in the reproductive characteristics of *C. ullrichi* among the three habitat types. However, we revealed that the life-history traits might be able to reflect seasonal changes (Table 9). It has been found that the young males and females with immature eggs show strong seasonality which might affect the overall abundance as well.

C. ullrichi occurs in wet, shady and also in dry, light forests of Slovakia (Kleinert 1983). In our study the species distinguished the habitats, i.e. occurring in higher number in the more opened oak forest, but it also used the other habitats. The results of investigations with *C. problematicus* showed that the beetles captured from different altitudes had different life strategies, at low altitude beetles being predominantly annual and at high altitude predominantly biennial (Sparks et al. 1995). It is possible that these differences can only be found on a large geographical scale. We found no differences between the seasonal and reproductive activity patterns of the beetles among the three different habitat types.

Based on our results, we propose that *C. ullrichi* has a functionally bimodal activity pattern. The early season activity peak is based on the high activity of females in May, because of the

reproductive period, while the late activity peak coincides with the high foraging activity of both sexes. This pattern was similar among the years, therefore the species has constant activity pattern in the studied forest habitats. Similarly to this species, large carabids in general with constant seasonality demonstrated less spatio-temporal variation in their activity densities (Andorkó et al. 2006). We also found that this species can reproduce only once per season with relatively low fecundity. These attributes make this species more sensitive to any stochastic event in its environment similarly to the large carabids, because their potential to respond to unfavourable or extreme environmental variation (i.e. fragmentation) may be limited.

4 Overall conclusion

In many European countries the habitat fragmentation has become relevant problem in the last twenty years. Changes in land use are considered to be the most important driver of global biodiversity loss (Sala et al. 2000; Buckley & Roughgarden 2004) and are also considered to be the most important threats for European forests. The forest practices had considerable effects on the ratio of the natural and semi-natural forests. Therefore, the monitoring and comparing of this kind of habitats is unavoidable and a very important skill (Eyre et al. 1996; Magura et al. 2000). The examinations of the ground-dwelling arthropod assemblages in the natural and semi-natural habitats are also essential, because these habitats have an important role in the recolonization of the regenerating habitats. The focus of most studies is at supra-individual level with their inevitable time constraints: effects on populations and assemblages need one or more generations to unfold. We studied the differences between two small forest fragments and the adjacent transition zone based on the abundance and species richness of carabids, because the spatial heterogeneity in these small habitat fragments may contribute to conserve the diversity of native biota. We found that ground beetle assemblages may reflect the small scale spatial heterogeneity among the different habitat types through the specific responses of the species, but most of the species use these habitats regardless the spatial variations: 1) the overall abundance and species richness were highest in the transition zone; 2) most of the species were characteristic of all habitat types; only few species was specific to any one habitat. The thinning as a forest management which was implemented before our study started was likely to highly influence the composition of the carabid assemblages inhabiting the area. The diversity increased during the twenty years in each habitat. Ten years after the completion of the forest practices (in the years of 1990s), we found significant differences neither in the abundance, nor in the species composition in the carabid assemblages. However, twenty years after the forest management (in 2005 and 2006), we found significant increases in the number of the majority of the large forest carabids, which might be the indicator of the increasing naturalness of these habitats. All these indicate the remarkable resilience of the carabid populations.

Organisms may also react to conditions in their habitats at lower organisational levels. Using life-history traits for ecological assessments might be beneficial due to the fact that these reflect better to the local environmental parameters than species richness and abundance.

These adaptations can be morphological or behavioural which makes these traits more suitable to track any changes in their environment (Nylin & Gotthard 1998). Therefore knowledge on life-histories of the study organisms in ecology is essential. According to Lövei & Magura (2006) superficial knowledge in this regard can easily derail ecological studies. Therefore it is necessary to contribute to our still-fragmentary knowledge on life histories.

While most of the recent papers concentrate on processes at community level, only few papers are concerned with the life-history traits and reproduction of carabids. Thus, we have tried to study the ground beetles at individual and also at supra-individual level. We found that *C. scheidleri* develops during one year, overwinters both as larva and as adult, adult females live more than one year, they reproduce more than once, and the different generations overlap during one season, assuring the persistence of the population. Old beetles participate also in the reproduction (Andorkó & Kádár 2004). According to Andorkó & Kádár (2009) *C. scheidleri* assures the persistence of the population at different levels and in different ways (e.g. the presence of old beetles in the reproduction, several reproductive periods in the same season, overlapping of the different generations, high number of ripe eggs per female). We also revealed that *C. ullrichi* is a typical spring breeder species with summer larvae and hibernates as adults. This species has one reproductive period in the season exclusively. The seasonal activity peaks and reproductive periods do not overlap. However *C. ullrichi* preferring the stable, deciduous forests where no such high habitat alterations occur, ensures the population's survival with the already mentioned spring breeder strategy. According to Fazekas (1997) the determination of the mandible wear proved to be the most precise method for age-estimation. According to Sparks et al. (1995) this ageing can be used for illustration only and not for age-estimation. Based on our experiences the determination of the mandible wear for age-estimation is an objective estimation, which is sex- and size-independent. In the case of *C. scheidleri*, we could estimate the age of the adults and also the type of overwintering, which were supported by the results of the dissection. Accordingly, age estimation based on mandible wear is a good age estimator when different generations of the species do not overlap, like in case of *C. ullrichi*. When generations overlap, the two age-estimations - the one based on mandible wear and the other on the developmental stage of the ovaries - together give good results. Therefore, if the age estimation based on mandible wear is supported by the results of the dissection, it could be a particularly precise method (Andorkó et al. 2005).

At individual/population level, our results are consistent with the suggestion that physiological state indicators could be a powerful early warning method of population decline during habitat change (Janin et al. 2011). Further, the complex interaction between tolerance limits, feeding conditions and stress levels during advancing habitat alteration underline the importance of using multiple criteria for assessing the impact of habitat fragmentation on biodiversity. Our results emphasize that carabids are also appropriate organisms for ecological studies on macroscale and landscape level as well. Based on the above mentioned facts we suggest careful consideration of the forest management practices in order to avoid further losses. We also propose that the long-term monitoring of assemblages is an efficient tool to improve our knowledge on insect population dynamics. These efforts correspond to the national conservation responsibilities, and Hungary is in the upper responsibility class due to the high ratio of unique habitat types and endemic species, especially of invertebrates (Schmeller et al. 2008). Moreover, our results prove Schmeller et al.'s (2008) initiative, that the identification and monitoring of biodiversity should require prioritization of conservation actions, such as (long-term) monitoring.

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7 Summary

Ground beetles are good ecological indicator species and many studies proved their sensitiveness to habitat alterations/disturbance. In the first part of the study we examined and showed how carabid assemblages react to the recovering of forest habitats in a long-term investigation, covering the period of twenty years (1986-2006). A total of 13 844 individuals belonging to 43 species were sampled in the Pilis Biosphere Reserve in three different habitat types (a beech forest, a transition zone between the two and an oak forest). According to our results there was a remarkable change in the species composition and activity density of ground beetles in these areas. The diversity was always the highest in the transition zone during all years. This zone possessed some species characteristics of both adjacent habitats, and that explained the high species richness of this site. We suggest that ground beetle assemblages may reflect the small spatial heterogeneity among the different habitat types, but most species use these habitats regardless the spatial variations. Regarding the temporal variation caused by the thinning as a forest management which was implemented one year before our study started, it was likely to highly influence the composition of the carabid assemblages inhabiting this area. As a consequence of it, the diversity of carabid assemblages increased during the twenty years in each habitat. Based on our experiences we believe that the identification and monitoring of biodiversity should require prioritization in conservation actions, such as (long-term) monitoring.

The second part of this thesis focuses on the life-history characteristics of two *Carabus* species containing data on their seasonal activities, age composition and reproductive characteristics. Based on our results, the studied *C. scheidleri* has evolved to persist in unstable environments and it is well adapted to the human disturbances by its long activity period, by several reproductive periods (high number of ripe eggs in ovaries/female, the presence of old beetles in the reproduction), by the ability of overwintering both as larvae and adults which can lead to overlapping generations. The other studied species *C. ullrichi* prefers the stable, deciduous forests where no such high habitat alterations occur, ensures the population's survival with „spring breeder strategy” and with the following life-history characteristics: one reproductive period per year, adult hibernation, low number of ripe eggs per female. Given that several species are protected, all the above mentioned information would be useful to harmonise conservation efforts during habitat management operations, like the use of chemicals in agricultural lands, forest management, etc., to minimise risk to non-

target ground beetles. Throughout their worldwide distribution and abundance they also prove a reliable snapshot about the conservation status of the studied habitat types.

8 Összefoglaló

A futóbogarak jó környezeti indikátorok, hiszen számos tanulmány bizonyította azok érzékenységét az élőhelyváltozásokra/zavarásokra. Ezen dolgozat első felében egy húsz éves (1986-2006) időszakot felölélő vizsgálatot mutatunk be: hogyan reagálnak, és hogyan változnak a futóbogár közösségek az erdészeti kezelések felhagyása utáni erdős területen. A vizsgált időszakon belül 43 fajt, és 13 844 egyedet csapdáztunk a Pilisi Bioszféra Rezervátum területén három különböző élőhelytípusban (egy bükkösben, egy tölgyesben és a közöttük elterülő átmeneti zónában). Az eredmények azt mutatták, hogy jelentős változás történt a fajösszetételben és a futóbogarak aktivitás denzitásában. A diverzitás minden esetben az átmeneti zónában volt a legmagasabb. A terület nagy fajdiverzitása azt jelzi, hogy ez a terület mind a két, szomszédos területről vonzott fajokat. A futóbogár közösségek a különböző élőhelytípusok között képesek jelezni a kismértékű térbeli heterogenitást, annak ellenére, hogy a legtöbb faj a területeket azok térbeli elkülönülése ellenére is használta. Az időbeli változások tekintetében a vizsgálatot megelőző évben befejezett erdészeti kezelés nagy valószínűséggel befolyásolta az itt élő futóbogár közösségek fajösszetételét. Ennek hatására a futóbogár közösségek diverzitása megnövekedett a húsz év során minden a három vizsgált területen. Az eredményeinkből arra következtethetünk, hogy a biológiai sokféleség feltárása és hosszútávú monitorozása elsőbbséget kell, hogy élvezzen a természetvédelmi kezelések tervezése során.

A dolgozat második része két *Carabus* faj életmenet jellemzőit tárja fel, azaz a szezonális aktivitásukat, a korösszetételt és a szaporodási jellemzőket vizsgáltuk. Az eredményeink azt mutatták, hogy a *C. scheidleri* képes az instabil környezetekben is fennmaradni, azaz jól alkalmazkodott az emberi zavarásokhoz. Mindezt a hosszú aktivitási időszakkal, a több szaporodási időszakkal (a nőstények petefészkében talált nagyszámú érett peteszám, a szaporodásban részt vevő idős nőstények jelenléte), a lárvaként és imágóként való áttelepés képességevel biztosítja. A különböző generációk átfednek. A másik vizsgált faj a *C. ullrichi* a stabil, lombhullató erdőket kedveli, ahol nem fordul elő jelentős élőhelyváltozás. A populáció túlélését az ún. „spring breeder” stratégiával biztosítja, amelynek feltételei közé tartoznak az alábbi életmenet jellemzők: évente egy szaporodási időszaka van, az imágók telelnek át, a nőstények petefészkében talált érett peték száma alacsony. Mivel számos faj védet, így a fent részletezett adatok hasznosak lehetnek az élőhelymegőrzési tervek elkészítésénél (például a mezőgazdasági területeken használt növényvédőszerek használatával kapcsolatban, vagy

egyes erdészeti kezelésekknél) annak érdekében, hogy a lehető legjobban megkíméljük ezeket a nem célszervezet futóbogárfajokat. A futóbogarak széles elterjedésük és abundanciájuk miatt a vizsgált területek konzervációs állapotának meghatározására is jól használhatóak.