

UNIVERSITY OF SOUTH BOHEMIA

IN ČESKÉ BUDĚJOVICE

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**Contrasting needs of grassland dwellers:
Habitat preferences of endangered beetles
(Coleoptera) on the Pouzdrany steppe**

MASTER THESIS

2010

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Pokluda, P., 2010: Contrasting needs of grassland dwellers: Habitat preferences of endangered beetles (Coleoptera) on the Pouzdrany steppe. MSc. Thesis, in English. – 69 p., Faculty of Science, The University of South Bohemia, České Budějovice, Czech Republic.

Annotation

The Master thesis presents results of study on habitat selection of flightless steppe beetles including darkling beetle *Blaps lethifera*, ground-beetle *Carabus hungaricus*, two longicorns (*Dorcadion* spp.), and four oil beetle species (*Meloe* spp.) using pitfall traps in dry-grassland fragment – the Pouzdrany steppe. This work provides description of their habitat preferences and seasonal activity pattern.

Statement

I hereby declare that I worked out this Master thesis on my own, or in collaboration with the co-authors of the presented manuscript, and only using the cited literature and under supervision of Mgr. Lukáš Čížek, Ph.D.

I declare that in accordance with the Czech legal code § 47b law no. 111/1998 in its valid version, I consent to the publication of my Master thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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V Českých Budějovicích, 30. dubna 2010

Acknowledgements

I am deeply grateful to my supervisor for help, valuable comments, fruitful scientific discussion, patience, and tolerance. In the first place I appreciate his friendly approach. I thank David Hauck for collecting notable portion of data and collaboration on field work. Jozef Dovala provided botanic data. I am grateful to Martin Konvička for valuable comments and assistance with statistical analyses. Many people helped with access to literature, among others I mention here Vítězslav Kubáň, Pavel Saska, and František Rosypal. I thank the Dočekal family for rendering accomodation, good wine, and base for field work. The study was supported by the Agency for Nature Conservation and Landscape Protection of the Czech Republic.

Abstract

The thesis presents study of habitat preference of eight endangered flightless steppe beetles sampled using pitfall traps in dry-grassland fragment – the Pouzdrany steppe. The studied species include darkling beetle *Blaps lethifera*, ground-beetle *Carabus hungaricus*, two longicorns (*Dorcadion* spp.), and four oil beetle species (*Meloe* spp.). We found that *C. hungaricus* prefers tall-grass patches with thick litter layer and is abundant on secondary biotopes. Although its abundance is positively correlated with moisture, the species avoids forest and woody habitats. *C. hungaricus* females prefer drier warmer sites than males, which broaden the range of habitats needed for this species. *Dorcadion fulvum* and *D. pedestre* prefer short-turf vegetation. *B. lethifera* exhibited affinity to patches of bare soil. *Meloe decorus* and *M. uralensis* prefer short-turf vegetation and patches of bare soil, while *M. proscarabaeus* prefers tall-grass vegetation in relatively humid conditions. The results demonstrate that co-occurring and often closely related species of flightless grassland beetles exhibit contrasting habitat requirements highlighting the necessity of spatially and temporarily diversified management of grasslands.

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PART I

Contrasting needs of grassland dwellers: Habitat preferences of endangered flightless beetles (Coleoptera)

1. INTRODUCTION

Temperate grasslands rank among the most threatened biomes on the Earth; ratio of their area converted by human activity to area protected is the highest among all the main biomes (Hoekstra et al., 2005). This applies also for Europe, where grasslands have been affected and endured due to long-term human land use (WallisDeVries et al., 2002; Cremene et al., 2005; Saarinen et Jantunen, 2005; Pärtel et al., 2007). However, agricultural intensification or abandonment caused their dramatic decline in both extent and quality during the 20th century (WallisDeVries et al., 2002; Cremene et al., 2005; Saarinen et Jantunen, 2005; Pärtel et al., 2007; Karlík et Poschlod, 2009; Stefanescu et al., 2009; de Bello et al., 2010; Woodcock et Pywell, 2010). In Central Europe, the process of grassland disappearance and degradation culminated during the second half of the 20th century (Mládek et al., 2006; Wittig et al., 2006; Woodcock et al., 2008; Karlík et Poschlod, 2009) when intensification was often augmented by collectivization and grassland acreage locally decreased to less than half its previous extent within just two decades (Skaloš, 2006). The extent of agricultural intensification was largest in lowlands, i.e. the most productive areas (Woodcock et al., 2008). Ceasing of pasture and hay production brought into lowlands by intensification of agriculture caused that most lowland grasslands were turned to arable land; remaining pastures and meadows suffered from increased stocking rates, artificial reseeded and heavily fertilization, or afforestation and abandonment followed by spontaneous overgrown by woody plants (Balmer et Erhardt, 2000; Konvička et al., 2005; Mládek et al., 2006).

Grasslands are biodiversity hotspots in Europe, especially for their high richness in plants, invertebrates, and birds (Pons et al., 2003; Pärtel et al., 2007; Sároszpataki et al., 2009; de Bello et al., 2010). Dry calcareous and steppic grasslands are of particular importance and hold great conservation value (WallisDeVries et al., 2002; Cremene et al., 2005; Saarinen et Jantunen, 2005; Karlík et Poschlod, 2009; Woodcock et Pywell, 2010). They are considered one of the most important habitat types for the conservation of insect diversity in Europe (cf. Van Swaay, 2002; WallisDeVries et al., 2002). Number of dry grasslands enjoys protection in many European countries. The conservation effort, however, often failed to stop the decline of grassland biodiversity (Van Swaay et Warren, 1999; WallisDeVries et al., 2002).

In Central Europe, dry grasslands are found mainly in lowlands, thus were heavily affected by recent land use changes. Most remaining steppe fragments are small and isolated; their biota subjects to tremendous extinction debt and experience severe decline (Konvička et al., 2005; Wenzel et al., 2006). At protected areas of Central Europe, a hands-off conservation

approach was frequently applied; conservationists often hailed the invasion of woody plants as the return of grasslands to their “natural state” (e.g. Veselý, 2002; Möllenbeck et al., 2009). The naive, biologically unjustified approach is responsible for degradation of most protected grasslands in, for example, former Czechoslovakia. Many steppe invertebrates of Central Europe thus went extinct at regional level (Gepp, 1994; Binot et al., 1998; Beneš et al., 2002; Farkač et al., 2005). In the Czech Republic, active conservation-oriented management of protected grasslands, such as mowing and pasture, started as late as in the 1980s (Veselý, 2002). Extent and intensity of the management is still not sufficient, therefore steppe-grasslands quality deteriorates, and their area further shrinks. There are, on the other hand, reports about excessively intensive, uniform conservation-oriented management of grasslands, often under the agri-environmental schemes, that seriously weakened populations of threatened species or led up to their extinction (Konvička et al., 2005; Konvička et al., 2008). Nature conservation is still searching for adequate measures to cope with loss of dry grasslands and their biodiversity.

In managing grasslands, the emphasis is usually placed on plants (Van Wieren et al., 1998; Konvička et al., 2008). Conservation-efficient grassland management needs to develop integrated approach that considers the requirements of plants and wide spectrum of animal taxa representing various life strategies (WallisDeVries et al., 2002). However, the amount of knowledge of various taxonomic groups as to occurrence and ecology is greatly biased (Clark et al., 2002). There is large body of information on plants and vertebrates, especially birds. Invertebrates are incomparably less studied; most attention is devoted to butterflies and orthopterans (Van Swaay, 2002; WallisDeVries et al., 2002; Badenhausser et al., 2009; Woodcock et al., 2010). Data on many groups, including flightless arthropods, are insufficient. Conservationists thus lack basic information on substantial portion of dry grasslands biota, which may compromise their effort to stop decrease of grasslands biodiversity.

I carried out a detailed survey on habitat selection of eight flightless grassland beetle species, i.e. churchyard beetle *Blaps lethifera* (Marsham, 1802), ground beetle *Carabus hungaricus* (Fabricius, 1792), two longicorn beetle species of genus *Dorcadion*, and four oil beetle species (genus *Meloe*). Nearly all the studied species are endangered and most are protected by national legislation; *C. hungaricus* is internationally protected under the Natura 2000 scheme. The information on their habitat requirements, crucial to their effective conservation, is missing. The study fills the gap in knowledge and helps to build the scientifically sound information base for conservation management of dry grasslands.

The study investigated following aspects of biology of the studied beetle species: (i) Effect of vegetation characteristics on their abundance at three different spatial scales. (ii) Effect of abiotic characteristics on their abundance. (iii) Comparison of their habitat selection. (iv) Patterns of seasonal activity.

2. MATERIALS AND METHODS

2.1 Study species

2.1.1 *Blaps lethifera*

A group of darkling beetle species near *B. lethifera* is taxonomically difficult and subjects to differing interpretations. The majority opinion is that four taxa, i.e. *B. milleri* (Seidlitz, 1894), *B. sinuaticollis* (Solier, 1848), *B. reflexicollis* (Solier, 1848), and *B. abdita* (Picka, 1978), represent synonyms of *B. lethifera* (Šustek, 1982; Novák, 2007). It is a Palearctic species; in Europe reaching the northern distribution border in British Isles, Norway, and Sweden; to south it reaches North Africa (Algeria, Tunisia, and Morocco), and to east Turkey and Kazakhstan in Asia (Picka, 1978; Ferrer et Picka, 1990; Vsevolodova-Perel' et Sizemskaya, 2007; Duff, 2008). It has been introduced to the USA (Warren et Steiner, 2008). It is a saprophagous species feeding on dead plant matter. *B. lethifera* acts as a synantropic species or occupies rodent burrows in European steppes (Picka, 1978). It is considered dry-steppe or desert-steppe species in Transural region and mesophilic-steppe species in Volgograd Province (Nagumanova, 2007; Vsevolodova-Perel' et Sizemskaya, 2007). To my knowledge, detailed information on its habitat requirements is not available.

2.1.2 *Dorcadion fulvum* and *D. pedestre*

Flightless longicorn beetles of Dorcadiini tribe probably represent the least investigated group of otherwise relatively well studied European Cerambycidae as their taxonomy, larval morphology, and bionomics are still unsatisfactorily known (Sláma, 1998; Sama, 2002). Their larvae develop underground, feeding on roots of herbaceous plants (Sama, 2002). Life cycle span varies from one to three years. Pupation occurs in the ground in an earthen cocoon, usually in the late summer of the second year. Adults overwinter in pupal cells and emerge in spring.

D. (Carinatodorcadion) fulvum (Scopoli, 1763) includes three subspecies in currently prevailing opinion (Sama, 2002). It is distributed in Central and south-eastern Europe, (Althoff et Danilevsky, 1997; Sama, 2002). The recent distribution in the Czech Republic is confined

to central and southern Moravia, where the species is most abundant on relatively humid meadows and pastures of lower elevations, but occupies also drier habitats such as steppes and vineyards (Sláma, 1998).

D. (Cribridorcadion) pedestre (Poda, 1761) is a monotypic species distributed in Central and south-eastern Europe (Althoff et Danilevsky, 1997; Sama, 2002). Its recent distribution in the Czech Republic is confined to southern Moravia, where the species occupies steppes, pastures, and other grasslands in lower elevations (Sláma, 1998).

Adults of both studied species occur from April to June, and are often encountered on tracks and paths (Sláma, 1998). The host plants of both species and the rates of their host specificity are unknown.

Although the studied species still represent the most widespread Dorcadiini in Central Europe, they experienced dramatic decline in the Czech and the Slovak Republics. Their distribution shrank to approximately half of that in the first half of the 20th century (cf. Sláma, 1998), yet they were not included in the Red List of the Czech Republic (cf. Farkač et al., 2005).

2.1.3 Oil beetles

Oil beetles of genus *Meloe* are part of blister beetles family (Meloidae). The family is known for its hypermetabolic development and parasitoid biology (see Bologna, 1991, for a review). Meloid hypermetaboly includes seven larval instars. The first instar larva called triungulin is adapted to reach its host, often by phoresy (Bologna et al., 2008). Genus *Meloe* parasitize bees (superfamily Apoidea) (Dvořák et Vrabec, 2007; Bologna et al., 2008). Data on host bee species and host specificity of individual oil beetle species are scarce or missing. Nearly all oil beetle species have phoretic triungulins (cf. Lückmann et Scharf, 2004; Lückmann, 2005; Bologna et al., 2008) that disperse to flowers and attach to passing bees. The bees carry them to their nests, where oil beetle larvae develop on pollen and nectar provisions, and the bee eggs and larvae (Hafernik et Saul-Gershenz, 2000; Saul-Gershenz et Millar, 2006). Triungulins sometimes exhibit cooperative behaviour and aggregate together on vegetation to mimic the appearance of a female bee and produce a chemical cue that mimics the sex pheromone of the female, luring males to land on them (pseudocopulation) (Hafernik et Saul-Gershenz, 2000; Saul-Gershenz et Millar, 2006). The larvae transfer to female bees during mating. For flightless oil beetles, the phoretic transport by bees represents the main mode of dispersal. Adult oil beetles feed on herbaceous plants. Females lack an ovipositor and lay eggs in chambers dug in the ground (Bologna et al., 2008). They produce

thousands to tens of thousands of eggs (Hafernik et Saul-Gershenz, 2000; Lückmann, 2006). Such a high reproductive rate is associated with high larval mortality.

The whole family Meloidae experienced dramatic decline in Central Europe, thus ranks to the most threatened groups of insects there (cf. Dvořák et Vrabc, 2007). Of 23 species historically reported for the Czech Republic, ten are considered extinct and another eleven are threatened with extinction (Vrabc, 2005a). In the Czech Republic, the genus *Meloe* is protected by law no. 395/1992.

M. (Micromeloe) decorus (Brandt et Erichson, 1832) is distributed from eastern France to Central Asia, known from all countries of Central Europe (Stebnicka, 1987; Dvořák et Vrabc, 2007). Adults occur from March to May (Vrabc, 1993; Švihla, 1996). Its triungulin was described by Bologna et Pinto (1995). Triungulins does not seem to be phoretic, contrarily to all other known oil beetle triungulins, and it is assumed that they find the nests of their hosts on their own (Vrabc et al., 2001; Lückmann et Scharf, 2004; Lückmann, 2005). To my knowledge, the bee hosts are unknown; knowledge on habitat selection by adults consists of vague reports, e.g. xerophilous grassy slopes or “xero-thermophilous species“ (Stebnicka, 1987; Švihla, 1996).

M. (Meloe) proscarabaeus (Linnaeus, 1758) is a Eurosiberian species widely distributed in Europe (Stebnicka, 1987; Švihla, 1996; Dvořák et Vrabc, 2007; Duff, 2008). Triungulins attack bees individually or form aggregations on plants possibly mimicking flowers (Klausnitzer, 2004). Adults occur from March to June (Vrabc, 2006). Although still considered one of the most widespread blister beetle species in the Czech Republic, *M. proscarabaeus* experienced dramatic decline during the 20th century as it has been recorded from only about 30 localities after 1990 (Vrabc, 2006). Its host species include plasterer bees (genus *Colletes*), mason bees (genus *Osmia*), and *Anthophora retusa* (Linnaeus, 1758); information on habitat selection of adults consists of vague reports, e.g. grassy slopes, forest edges, balks, or “xero-thermophilous species“ (Liston, 1979; Stebnicka, 1987; Knight, 1995; Švihla, 1996).

M. (Eurymeloe) scabriusculus (Brandt et Erichson, 1832) is distributed from eastern France to Central Asia, known from all countries of Central Europe (Stebnicka, 1987; Dvořák et Vrabc, 2007). Its triungulin was described by Lückmann et Scharf (2004). Adults occur from April to May (Stebnicka, 1987; Švihla, 1996). In the Czech Republic it is found in lower elevations of Bohemia and Moravia, but details on distribution are missing. To my knowledge, the host species are unknown; knowledge on habitat selection of adults consists of

vague reports, e.g. grassy slopes, balks, or “xero-thermophilous species“ (Stebnicka, 1987; Švihla, 1996).

M. (Micromeloe) uralensis (Pallas, 1777) is a species ranging from the Pannonian region to Central Asia; (Dvořák, 1983; Dvořák et Vrabc, 2007). Its triungulin was described by Lückmann et Scharf (2004). Triungulins of *M. uralensis* are very similar to those of *M. decorus* and both species belong to the subgenus *Micromeloe*; it is thus assumed that triungulins of *M. uralensis* are not phoretic (di Giulio et al., 2002; Lückmann et Scharf, 2004). Adults occur from April to May (Švihla, 1996). *M. uralensis* is considered critically endangered in the Czech Republic (Farkač et al., 2005). It was historically reported from six localities in southern Moravia (Vrabc, 2004; 2005b). Although Vrabc (2004; 2005b) reports Pouzdrany steppe as the only one recent locality in the country, the species has been found in five other sites of southern Moravia during the last years (unpublished data; M. Holomčík, pers. comm.; S. Krejčík, pers. comm.; M. Škorpík, pers. comm.). These sites represent loess or limestone steppe fragments, agricultural land (vineyards, orchards, field margins), or combination of both. To my knowledge, the host species are unknown; knowledge on habitat selection of adults consists of vague reports, e.g. steppes, or “xero-thermophilous species“ (Švihla, 1996).

2.2 Study site

The study site was Pouzdrany steppe and its vicinity (48°56'18" – 48°56'54"N; 16°38'12" – 16°38'49"E; 200-300 m a.s.l.), about 25 km south of the Brno city in southern Moravia, Czech Republic. This National Nature Reserve and Site of Community Importance (total area: 180.8 ha) represents one of the largest remnants of subcontinental steppic grasslands in the region, characterized mainly as Pannonic loess steppe, subcontinental steppe, and forest-steppe. It is renowned as regional stronghold of Pannonian biota. Its parts are overgrown with shrubs and trees due to cessation of pasture and hay production after the Second World War. After establishing the NNR in 1956 hands-off conservation approach was applied. Only occasional fires together with numerous European rabbits (*Oryctolagus cuniculus*) prevented successional overgrowth of some parts of the steppe. An active management, consisting of sheep grazing and mowing, was partly reestablished in the 1990s. At present the vegetation forms a mosaic of various seral stages of grasslands, occasional solitary trees, shrubs, and patches of shrubland and woodland. The steppe is surrounded by agricultural land (arable land, vineyards, orchards) and formerly coppiced deciduous forest.

The topography is rugged, the bedrock consists of Palaeogene calcareous claystone and sandstone, partly covered by Pleistocene loess (for details see Adamová, 1988; Mackovčín et al., 2007). The climate is relatively warm and dry; mean annual temperature in a nearby town of Hustopeče is 9.2 °C, mean annual rainfall nearly 500 mm (for details see Mackovčín et al., 2007).

2.3 Sampling

Beetles were sampled using a capture-and-release approach with beer-baited pitfall traps. A total of 167 traps were positioned across the steppe and in its vicinity, distributed at various distances but keeping 5 m as a minimum. Sampling covered a wide range of habitats and vegetation types, including (roughly classified): fallow land (9), shortgrass steppe (19), tall-grass vegetation (100), shrubby vegetation on the steppe (16), dry forest steppe (13), and mesophilous forest steppe (10). Traps were active between March 26th and November 6th, 2006. The trapping covered the whole activity period of most of the studied beetles in the year 2006 as the site was covered by compact snow cover a few days before installation of traps and the first snow fell down just after their removing. Traps were inspected 1–2 times a week, summing 45 inspections in total. Beetles were released 2 m from the respective trap.

Captures of the above eight beetle species (see Table 1), the trap position, and the inspection date were recorded. Gradient of slope was measured using an angle gauge. Characteristics of surrounding vegetation were collected or estimated by an experienced botanist.

2.4 Variables

The following beetle, vegetation, and abiotic variables were used:

Beetle variables: (i–viii) abundances of the eight beetle species – total number of captures of a given beetle species in each trap during the study period.

Vegetation variables: Relative covers (in %) of the following vegetation characteristics and selected indicative or otherwise noteworthy plants were estimated on three spatial scales (1 m, 5 m, and 10 m, within circles of the respective diameter with trap in the centre): (i) bare soil (100% minus total vegetation); (ii) herbs and grasses; (iii) broad-leaved herbs; (iv) short grass (< 20 cm); (v) tall grass (> 20 cm); (vi) short dicots (< 20 cm); (vii) tall dicots (> 20 cm); (viii) tussock grass; (ix) non-tussock grass; (x) litter; (xi) short shrubs (< 50 cm); (xii) high shrubs (> 50 cm); (xiii) trees; (xiv) woody plants (pooled variables xii and

xiii); (xv) feather grasses (*Stipa* spp.) – a dominant steppic grass; (xvi) licorice (*Glycyrrhiza glabra*) – an exotic invasive species; (xvii) wood small-reed (*Calamagrostis epigejos*) – a native species invading grasslands. Variables vi–ix lack 10 m scale since their estimation is reliable on short distances only.

Abiotic variables: (i) temperature; (ii) humidity; (iii) soil reaction; (iv) soil nitrogen content; (v) light; (vi) salinity; (vii) gradient of slope (in degrees). Values of variables i–vi were estimated using plant-species data from plot around each trap (circle, 1 m diameter). The dataset contained 160 plant species in total. The variables were obtained using ordinal plant indicator values (Ellenberg et al., 1992) that describe the ecological requirements of Central European vascular plants and correlate well with measured values (Schaffers et Sýkora, 2000). We used values given by Borhidi (1995) for the Hungarian flora, summarized by Horváth et al. (1995), since Ellenberg's original list does not encompass all the species we identified. The Borhidi values range from 1 to 9 for all variables except for humidity (1–12) and salinity (0–9). The higher the Borhidi value, the higher the level of a given characteristic. The value of each abiotic variable for each trap was calculated as an arithmetic mean of indicator values of all plant species recorded from a plot as recommended by Käfer et Witte (2004).

2.5 Analyses

Using regression and multivariate analyses, we investigated effects of vegetation and abiotic variables on the abundance of individual beetle species, and we compared habitat preferences of the sampled beetle species. In all analyses, traps represented samples characterized by abundances of sampled beetle species, surrounding vegetation, and abiotic factors.

The effect of vegetation on the given beetle species abundance was investigated using Generalized Linear Models (GLM). To establish spatial scale of the vegetation variables with the highest effect on the given beetle species abundance, full models (quasipoisson distribution of residual variability, log link function, explanatory variables log-transformed) were separately fitted for the vegetation variables on the three spatial scales (1 m, 5 m, 10 m). Only the vegetation variables (i–v) and (x–xvii), estimated for all the three spatial scales, were used as explanatory variables. The models were compared using the model deviance information (= explained variability) and Mallows' Cp statistic. After selecting the spatial scale with the best explanatory power for the given beetle species, all the vegetation variables

estimated for that scale entered further analyses. Their independent effects on abundance of the given beetle species were assessed using F-test (GLM, quasipoisson distribution of residual variability, log link function, explanatory variables log-transformed). *C. hungaricus* was omitted in these analyses as it was investigated in detail by Pokluda et al. (submitted, Part II of the thesis).

Relations of vegetation variables were investigated using an unconstrained linear ordination, the principal component analysis (PCA). Data were log-transformed. Scaling focused on inter-species correlations, species scores were divided by standard deviations, species data were centered, samples were neither centered nor standardized.

Independent effects of the abiotic variables on the abundance of each beetle species were investigated using F-test (GLM, quasipoisson distribution of residual variability, log link function). *C. hungaricus* was omitted in these analyses as it was investigated in detail by Pokluda et al. (submitted, Part II of the thesis). Rank correlation coefficients between abiotic variables were calculated.

Relations of habitat preferences of studied beetle species were investigated using an unconstrained linear ordination, the principal component analysis (PCA). Abundance data of each species were square-root transformed. Scaling focused on inter-species correlations, species scores were divided by standard deviations, species data were centered, samples were neither centered nor standardized.

Regression analyses were carried out using R 2.7.2 (Dalgaard, 2002; Maindonald et Braun, 2003), multivariate analyses using Canoco for Windows 4.5 (ter Braak et Šmilauer, 2002; Lepš et Šmilauer, 2003), and correlation coefficients were calculated using Statistica 9.1 StatSoft, Inc. (Hill et Lewicki, 2006).

3. RESULTS

In total, 4143 captures of the eight studied beetle species were recorded (individual species abundances see in Table 1).

3.1 Habitat preferences

Abundance of *B. lethifera* was positively affected by extent of bare soil and negatively influenced by covers of herbs and grasses and tall grass at the 5 m scale. The negative effect of non-tussock grass was marginally significant. Abundance of *D. fulvum* was negatively affected by cover of high shrubs at the 5 m scale. The positive effects of covers of short grass

and tussock grass and the negative effect of cover of wood small-reed were marginally significant. Abundance of *D. pedestre* was positively affected by covers of broad-leaved herbs, short grass, and short dicots and negatively influenced by covers of tall grass and litter at the 5 m scale. Abundance of *M. decorus* was negatively affected by cover of tall grass at the 1 m scale. The positive effects of cover of short grass and extent of bare soil were marginally significant. Abundance of *M. proscarabaeus* was positively affected by covers of broad-leaved herbs and tall dicots and negatively influenced by cover of tussock grass at the 1 m scale. Abundance of *M. scabriusculus* was negatively affected by cover of high shrubs at the 1 m scale, the effect was marginally significant. Abundance of *M. uralensis* was positively affected by covers of short dicots and feather grasses, and negatively influenced by cover of wood small-reed at the 5 m scale. The positive effect of bare soil extent and the negative effects of covers of tall grass and non-tussock grass were marginally significant (see Table 2 for details).

The PCA ordination comparing distribution of vegetation characteristics distinctly separated three groups of variables (Figure 1). The first (horizontal) axis separated variables indicating short-turf steppe with bare soil patches or feather grasses growths, i.e. tall-grass vegetation with numerous bare soil patches, from variables indicating tall-grass steppe with litter, partly degraded by invasive plants. The second (vertical) axis separated woody plant variables. The first axis thus describes a gradient from short-grass steppe with bare soil to tall-grass steppe with high herb cover, whereas the second axis represents a gradient from short to high woody plants. The 5 m scale was selected as it had the best explanatory power for the most beetle species, contained all the vegetation variables, and accounted for the highest amount of variability on the first two ordination axes.

No relation between abundance of *B. lethifera* and abiotic factors was found. Abundance of *D. fulvum* was negatively affected by inclination, humidity, and soil nitrogen content; the effects of humidity and soil nitrogen content were marginally significant. Abundance of *D. pedestre* was negatively affected by soil nitrogen content and inclination; both effects were marginally significant. Abundance of *M. decorus* was positively affected by soil reaction and light; the effect of light was marginally significant; *M. proscarabaeus* was positively affected by soil nitrogen content and humidity and negatively influenced by soil reaction; the effect of humidity was marginally significant. Abundance of *M. scabriusculus* was positively affected by soil reaction and light; the effect of light was marginally significant. Abundance of *M. uralensis* was positively affected by temperature and soil reaction and negatively influenced by humidity and soil nitrogen content; the effect of soil

nitrogen content was marginally significant (see Table 3 for details). Most of the abiotic habitat characteristics exhibited strong correlations (see Table 4 for details).

In the PCA ordination comparing habitat preferences of the studied beetles (Figure 2), the first (horizontal) axis separated species of short-turf habitats, i.e. *D. pedestre*, *D. fulvum*, and *M. uralensis*, from tall-grassland preferring *C. hungaricus* and *M. proscarabaeus*. The second (vertical) axis separated *B. lethifera*, *M. decorus*, and *M. uralensis* from other species. The first axis thus describes a gradient from short-grass vegetation to tall-grass steppe, whereas the second axis represents a gradient of bare soil extent. The first axis accounted for approximately ten times more variability than the second one.

3.2 Seasonal activity

Adults of oil beetles occurred from the beginning of the sampling (March 26th) to May 20th. Individual species differed in duration and timing of their activity periods. *M. decorus*, *M. proscarabaeus*, and *M. uralensis* occurred from the late March, activity of *M. scabriusculus* started at the beginning of April. The activity of *M. decorus* and *M. uralensis* ceased on April 17th and April 23th respectively; activity of *M. proscarabaeus* ceased on May 12th, and the last *M. scabriusculus* individual was found on May 20th (see Figure 3 for details).

B. lethifera occurred continually from the spring to the beginning of October. *D. fulvum* occurred from the middle of May to the beginning of July (maximum between the middle of May and the middle of June), and *D. pedestre* occurred from the third decade of April to the second decade of June (maximum between the end of April and the beginning of June).

4. DISCUSSION

4.1 Habitat preferences

The studied beetles exhibit various, partly overlapping habitat needs. Their preferences rank among three main grassland habitat types, i.e. relatively humid tall-grass steppe, dry short-turf vegetation, and/or patches of bare soil.

B. lethifera exhibited the strongest preference for bare soil among all the vegetation characteristics and also among all the species studied. This is also supported by negative effects of covers of herbs and grasses, tall grass, and non-tussock grass on its abundance. Influence of any abiotic characteristic was not detected. *B. lethifera* often occupies burrows of

rodents (Picka, 1978), where the microclimate is stable and rather independent on that on soil surface. Burrow entrance is usually surrounded by bare ground and short-turf vegetation. The studied population of *B. lethifera*, however, hardly depends solely on burrows. The study site was nearly burrows-free during the study period as population of European rabbits is reduced to a few individuals since 1993, and European ground squirrel (*Spermophilus citellus*) went extinct in the 1980s or the 1990s (Š. Hulová, pers. comm.).

D. fulvum is a species of open habitats (Sláma, 1998). It is corroborated by its avoidance of high shrubs. It prefers short turf to tall grassland, as the negative effect of wood small-reed also indicates. The positive effect of cover of tussock grass on *D. fulvum* suggests its preference for bare soil patches. The described habitat selection is further supported by *D. fulvum* preference for drier sites with less soil nitrogen content. It is important to note that the species is not very abundant within the study site generally. According to Sláma (1998) the species is abundant on relatively humid meadows and less numerous on drier habitats. It is possible that its detected preference for abiotic factors is biased by lack of more suitable habitat, i.e. relatively humid short-turf conditions. The negative effect of inclination on *D. fulvum* abundance is difficult to interpret; it may represent sampling artifact as the species was captured just within small area of the study site.

D. pedestre prefers short-turf vegetation within the study site as its abundance was positively affected by covers of short grass, short dicots, and broad-leaved herbs and negatively influenced by cover of tall grass and litter. It is also supported by its preference for sites with lower soil nitrogen content that are drier within the study site. The negative effect of inclination on abundance of *D. pedestre* is difficult to interpret. It may represent sampling artifact as in the case of *D. fulvum*.

M. decorus prefers short-turf vegetation with patches of bare soil within the study site. This is corroborated by the positive effects of light and pH on its abundance. It confirms the opinion of Švihla (1996) that it is a xero-thermophilous species as sites with higher pH and solar radiation are also drier within the study site. As triungulins of *M. decorus* are assumed not to be phoretic and find the host nests on their own (Vrabec et al., 2001; Lückmann et Scharf, 2004; Lückmann, 2005; but see Vrabec, 2005b), habitat selection of *M. decorus* adults thus likely reflects the distribution of nests of its hosts more markedly than habitat selection of adults of most other oil beetle species. Interpretation of the detected habitat preference is difficult due to lack of knowledge on host bee species. While phoretic triungulins easily cover large distances attached to other insects, the non-phoretic triungulins of *M. decorus* would imply low mobility of the species. The assumption of non-phoretic triungulins is contradicted

by the rapid spread of *M. decorus* to number of distant and isolated sites in the Czech Republic after 1990 (Vrabec, 1993; 2002; 2005a; 2005b). It seems unlikely that the species would inhabit numerous sites undetected for decades. I therefore consider it likely that *M. decorus* triungulins are at least occasionally phoretic, which allowed for the recent spread of the species (e.g. Vrabec, 2005b). Further studies investigating phoresy and development of the species are needed.

M. proscarabaeus prefers tall-grass vegetation within the study site as its abundance was positively affected by covers of broad-leaved herbs and tall dicots. Tussock grass, represented mostly by xerophilous grasses within the study site, had the negative effect on the species abundance. These preferences are corroborated by habitat selection for abiotic factors, i.e. the positive effects of soil nitrogen content and humidity and the negative effect of pH on abundance of *M. proscarabaeus*. This contradicts the opinion of Švihla (1996) that *M. proscarabaeus* is a xero-thermophilous species. Habitat selection of *M. proscarabaeus* adults is probably affected by distribution of nests where they have developed, distribution of their food plants, distribution of flowering plants pollinated by host bees, or combinations of these factors. To attribute the distribution of *M. proscarabaeus* to that of its hosts is difficult as the beetle exploits wide range of bee species (Liston, 1979; Stebnicka, 1987; Knight, 1995). Habitat preference of *M. proscarabaeus* starkly differs from those of the other oil beetle species studied; *M. proscarabaeus* is the least xerophilous. The species distribution in the Czech Republic is probably reflected by this pattern as it is the most widespread of the oil beetle species studied (Vrabec, 2006). However, the dramatic decline experienced by *M. proscarabaeus* during the 20th century (Vrabec, 2006) can indicate that its habitat and/or its hosts are declining.

M. scabriusculus exhibited poor response to vegetation characteristics, probably due to low sample size. Its abundance was negatively affected by cover of high shrubs, which simply confirms the general notion that it is a species of open habitats (Stebnicka, 1987). The positive effects of pH and especially light on its abundance confirm that *M. scabriusculus* is a xero-thermophilous species (Švihla 1996).

M. uralensis prefers short-turf vegetation, patches of bare soil and feather grasses, i.e. xerophilous tall-grass tussock vegetation with patches of bare soil. This is further supported by its avoidance of wood small-reed, tall grass, and non-tussock grass and habitat selection for abiotic factors, i.e. the positive effects of temperature and pH and the negative effects of humidity and soil nitrogen content on its abundance. These findings support the opinion that it is a xero-thermophilous species (Švihla, 1996). The habitat selection of *M. uralensis* adults is

thus very similar to that of *M. decorus*. Due to absence of knowledge on host species, interpretation of the detected habitat preferences remains difficult. Triungulins of *M. uralensis* are assumed not to be phoretic (Lückmann et Scharf, 2004), which is likely to affect its biology in a similar way as in the above-discussed *M. decorus*.

In analyses investigating explanatory powers of vegetation variables on 1 m, 5 m, and 10 m spatial scales, the 1 m or the 5 m scales exhibited the highest explanatory power for distribution of individual species. This corresponds to the pattern of habitat use of individual species and probably also to their mobility. From this point of view two groups of species are differentiated; species of rather low mobility of adults, i.e. oil beetles *M. decorus*, *M. proscarabaeus*, and *M. scabriusculus*, and species of higher one, i.e. churchyard beetle *B. lethifera*, ground-beetle *C. hungaricus* (see Pokluda et al., submitted, Part II of the thesis), longicorns *D. fulvum* and *D. pedestre*, and oil beetle *M. uralensis*. These findings suggest that there is no universal spatial scale for collecting the vegetation data around pitfall traps if sampling flightless grassland beetles. The 1 m to 5 m scales, however, are probably suitable for most species.

4.2 Seasonal activity

Our data allow for investigation relations between habitat selection and temporal patterns of activity of studied beetle adults within the study site. *B. lethifera* and *C. hungaricus* are long-lived and occur from the spring to the late fall (Pokluda et al., submitted, Part II of the thesis). *M. proscarabaeus*, the oil beetle preferring relatively humid habitats, had the longest period of activity of all the oil beetle species. Adult activity of *M. decorus* and *M. uralensis*, i.e. species exhibiting distinct preference for xeric habitats, was concentrated to the early spring and lasted for less than a month. Although *M. scabriusculus* preferring similar habitats occurred later than *M. decorus* and *M. uralensis*, it was also found for relatively short period. I therefore hypothesize, that in comparison to mesophilous species, inhabitants of xeric habitats have shorter life span and/or are active earlier in the season, perhaps due to warmer conditions. This is further supported by the fact that the more xerophilous *D. pedestre* occurred earlier than the more mesophilous *D. fulvum*.

Some of the studied oil beetle species occur within the study site since February or even January, depending on weather in actual year (unpublished data). The winter preceding the study period was extremely cold and the site was covered by compact snow cover up to a few days before the beginning of the study period. Onset of *Meloe decorus*, *M.*

proscarabaeus, and *M. uralensis* activity was missed by a few days as they all were observed during trap installation.

4.3 Management recommendations

The Pouzdrany steppe represents a biodiversity hotspot of international importance. It serves as an habitat island within extensive agricultural landscape to populations of many threatened invertebrate and plant species, some of them having there the last or one of the last populations in the region, e.g. *C. hungaricus*, *M. uralensis*, predatory bush cricket (*Saga pedo*), and *Artemisia pancicii* (Grulich, 2004; Dvořák et al., 2008). The site represents north-western margin of current distributional ranges of many species. Suitable management of the site is therefore crucial to sustain local and regional biodiversity. The below discussed recommendations, however, apply also to other dry-grasslands fragments.

Our results demonstrate that among the eight species of flightless dry-grassland beetles various habitat needs are encountered; even the closely related, locally co-occurring oil beetle species exhibit strikingly different patterns of habitat use. For their survival, the studied species require wide range of microhabitats including relatively humid tall-grass steppe, xeric tussock tall-grass vegetation, xeric short-turf vegetation, and patches of bare soil.

While tall-grass and “overgrowing” steppe vegetation covers most of the site at present, the short-turf vegetation and bare soil patches occupy small proportion of its area. The bare soil is currently restricted to paths, tracks, surroundings of rabbit burrows, molehills, or patches between tussocks; the short-turf vegetation is limited to the driest and the most trampled parts of the site. Given the importance of bare soil patches and short-turf vegetation for sustaining local populations of highly threatened invertebrates including *M. uralensis*, *M. decorus*, *D. pedestre*, *D. fulvum*, and *B. lethifera*, it is necessary to increase their extent within the site. For the sake of *D. fulvum* and possibly other species with similar requirements, the short-turf vegetation should be restored also on more humid parts of the locality. On the other hand, *M. proscarabaeus* and *C. hungaricus* prefer tall-grass and high vegetation cover (Pokluda et al., submitted, Part II of the thesis), and it is necessary to accommodate also their needs.

The site management should include temporarily varying rotational grazing accompanied by mowing, support of local rabbit population, prescribed burning, and soil disturbance. Grazing intensity should vary as intensive grazing creates short-turf vegetation and bare soil patches. Sizeable proportions of the locality should be left unmanaged for 5–10

years, to allow for regeneration of tall-grass conditions, but to prevent succession towards scrub. For patches overgrown by woody vegetation, partial cutting followed by winter prescribed burning is the most efficient method of grassland restoration (Möllenbeck et al., 2009), if they can be easily recolonised and are not under immediate threat of invasion by fire-tolerant plants, such as wood small-reed (Borkowski, 2004). Invasive woody species should be removed without exception, indigenous species selectively, leaving solitary individuals or small groups untouched.

5. CONCLUSIONS

Insects inhabiting identical habitat, such as dry grasslands, often differ in finer-level habitat requirements. It makes managing isolated insular remnants of rare habitats particularly challenging (Balmer et Erhardt, 2000; Bourn et Thomas, 2002; WallisDeVries et al., 2002). There is an increasing consensus that the spatially and temporarily diversified, rotational patch management is the most appropriate approach in managing isolated grasslands to retain high local diversity (Balmer et Erhardt, 2000; WallisDeVries et Raemakers, 2001; WallisDeVries et al., 2002; Pöyry et al., 2004; Konvička et al., 2005; Saarinen et Jantunen, 2005; Schmidt et al., 2008). The contrasting habitat requirements of the studied species support this general rule of grassland management.

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7. APPENDICES

Table 1. Number of captures (n) and conservation status (CS) of beetle species sampled using pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic between March 26th and November 6th, 2006.

Beetle species	n	CS ^a
Darkling beetles (Tenebrionidae)		
<i>Blaps lethifera</i> (Marsham, 1802)	100	
Ground beetles (Carabidae)		
<i>Carabus hungaricus</i> (Fabricius, 1792)	3819	VU
Longicorn beetles (Cerambycidae)		
<i>Dorcadion fulvum</i> (Scopoli, 1763)	25	D
<i>Dorcadion pedestre</i> (Poda, 1761)	25	D
Oil beetles (Meloidae)		
<i>Meloe decorus</i> (Brandt et Erichson, 1832)	44	
<i>Meloe proscarabaeus</i> (Linnaeus, 1758)	54	EN
<i>Meloe scabriusculus</i> (Brandt et Erichson, 1832)	16	NT
<i>Meloe uralensis</i> (Pallas, 1777)	60	CR

^a Status in the Czech Republic according to Farkač et al. (2005) follows IUCN Red List categories (CR – critically endangered, EN – endangered, VU – vulnerable, NT – nearly threatened) or species is considered declining (D; cf. Sláma, 1998).

Table 2. Effect of vegetation on abundance of individual beetle species at pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. Independent effects of the relative cover of vegetation characteristics in trap surroundings (within circle of the given diameter) on number of captures of individual species, as returned by F-test (GLM, quasipoisson distribution of residual variability, log link function, explanatory variables log-transformed, n = 167). The spatial scales for individual species were selected using model deviance information (amount of explained variability) and Mallows' Cp statistic of full models separately fitted for the vegetation variables on scales of 1 m, 5 m, and 10 m. Only significant results are shown.

Model	coefficient	df	Residual deviance	Model deviance	F	p
<i>Blaps lethifera</i> 5 m						
null		166	244.5			
bare soil	1.00	1, 165	221.4	23.2	13.79	***
herbs and grasses	-1.26	1, 165	229.9	14.7	8.38	**
tall grass	-0.55	1, 165	231.1	13.5	6.94	**
non-tussock grass	-0.26	1, 165	233.8	10.7	4.94	*
<i>Dorcadion fulvum</i> 5 m						
null		166	123.7			
high shrubs	-166.69	1, 165	102.4	21.3	17.84	****
short grass	0.57	1, 165	113.9	9.8	6.09	*
tussock grass	0.70	1, 165	114.1	9.6	5.84	*
<i>Calamagrostis epigejos</i>	-1.15	1, 165	115.5	8.3	5.17	*
<i>Dorcadion pedestre</i> 5 m						
null		166	173.3			
tall grass	-2.21	1, 165	110.5	62.8	31.41	*****
broad-leaved herbs	2.70	1, 165	114.1	59.3	26.47	*****
short grass	1.11	1, 165	140.1	33.2	10.68	**
litter	-4.08	1, 165	145.7	27.6	7.60	**
short dicots	0.90	1, 165	141.8	31.5	6.87	**
<i>Meloe decorus</i> 1 m						
null		166	152.7			
tall grass	-0.42	1, 165	143.4	9.3	7.40	**
short grass	0.30	1, 165	146.4	6.3	4.94	*
bare soil	0.56	1, 165	147.2	5.5	4.16	*
<i>Meloe proscarabaeus</i> 1 m						
null		166	280.0			
tussock grass	-0.66	1, 165	243.3	36.7	10.58	**
tall dicots	0.71	1, 165	249.6	30.4	7.63	**
broad-leaved herbs	1.21	1, 165	249.8	30.2	6.85	**
<i>Meloe scabriusculus</i> 1 m						
null		166	77.8			
high shrubs	-20.06	1, 165	73.7	4.1	4.51	*
<i>Meloe uralensis</i> 5 m						
null		166	225.6			
short dicots	0.57	1, 165	198.3	27.3	15.17	***
<i>Stipa</i> spp.	0.49	1, 165	201.5	24.1	11.04	**
<i>Calamagrostis epigejos</i>	-0.91	1, 165	208.9	16.7	7.69	**
tall grass	-0.72	1, 165	211.2	14.4	6.51	*
non-tussock grass	-0.33	1, 165	214.9	10.7	4.71	*
bare soil	0.83	1, 165	215.4	10.2	4.36	*

*p < 0.05; **p < 0.01; ***p < 0.001; ****p < 0.0001; *****p < 0.00001

Table 3. Effect of abiotic characteristic on abundance of individual beetle species at pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. Independent effects of the abiotic characteristics of trap surroundings (circle of 1 m diameter) on number of captures of individual species, as returned by F-test (GLM, quasipoisson distribution of residual variability, log link function, n = 167). Only significant results are shown.

Model	coefficient	df	Residual deviance	Model deviance	F	p
<i>Dorcadion fulvum</i>						
Null		166	123.7			
degree of slope	-0.11	1, 165	105.7	18.0	12.35	***
humidity	-1.92	1, 165	113.3	10.4	6.44	*
soil N content	-1.55	1, 165	112.3	11.4	5.55	*
<i>Dorcadion pedestre</i>						
null		166	173.3			
soil N content	-2.33	1, 165	153.5	19.8	5.51	*
degree of slope	-0.13	1, 165	150.7	22.7	5.09	*
<i>Meloe decorus</i>						
null		166	152.7			
pH	1.88	1, 165	144.2	8.5	6.92	**
light	1.52	1, 165	146.6	6.2	4.78	*
<i>Meloe proscarabaeus</i>						
null		166	280.0			
soil N content	1.19	1, 165	205.1	75.0	33.42	****
pH	-2.15	1, 165	242.7	37.3	8.76	**
humidity	1.65	1, 165	247.2	32.8	6.40	*
<i>Meloe scabriusculus</i>						
null		166	77.8			
pH	3.20	1, 165	70.0	7.9	8.32	**
light	2.26	1, 165	73.0	4.8	5.04	*
<i>Meloe uralensis</i>						
null		166	225.6			
temperature	2.48	1, 165	197.4	28.2	13.28	***
humidity	-1.86	1, 165	202.1	23.6	11.72	***
pH	2.24	1, 165	209.7	15.9	7.46	**
soil N content	-0.98	1, 165	211.3	14.3	6.62	*

*p < 0.05; **p < 0.01; ***p < 0.001; ****p < 0.00001

Table 4. Rank correlation coefficients between abiotic variables (right upper corner) and their significances (left lower corner).

	temperature	humidity	pH	soil N content	light	salinity	degree of slope
temperature	—	-0.67	0.69	-0.51	0.59	-0.11	0.28
humidity	*****	—	-0.67	0.84	-0.58	-0.04	-0.27
pH	*****	*****	—	-0.65	0.42	-0.31	0.22
soil N content	*****	*****	*****	—	-0.48	0.03	-0.15
light	*****	*****	*****	*****	—	0.22	0.19
salinity	n.s.	n.s.	****	n.s.	**	—	0.01
degree of slope	***	***	**	n.s.	*	n.s.	—

n.s.: p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001; ****p < 0.0001; *****p < 0.00001

Figure 1. PCA ordination comparing distribution of vegetation characteristics estimated within circle of 5 m diameter around pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. The first ordination axis accounted for 26.6 % and first two axes for 42.9 % of the total variability (eigenvalues of first to fourth axes: 0.266; 0.163; 0.115; 0.107). All the variables and samples (167) entered analysis, variables with minimum fit = 6 are depicted. A clear separation of variables indicating short-turf steppe with bare soil patches or *Stipa* spp. growths, i.e. tall-grass vegetation with numerous bare soil patches, from variables indicating tall-grass steppe with litter, partly degraded by invasive plants (horizontal axis), and woody plant variables (vertical axis) is apparent.

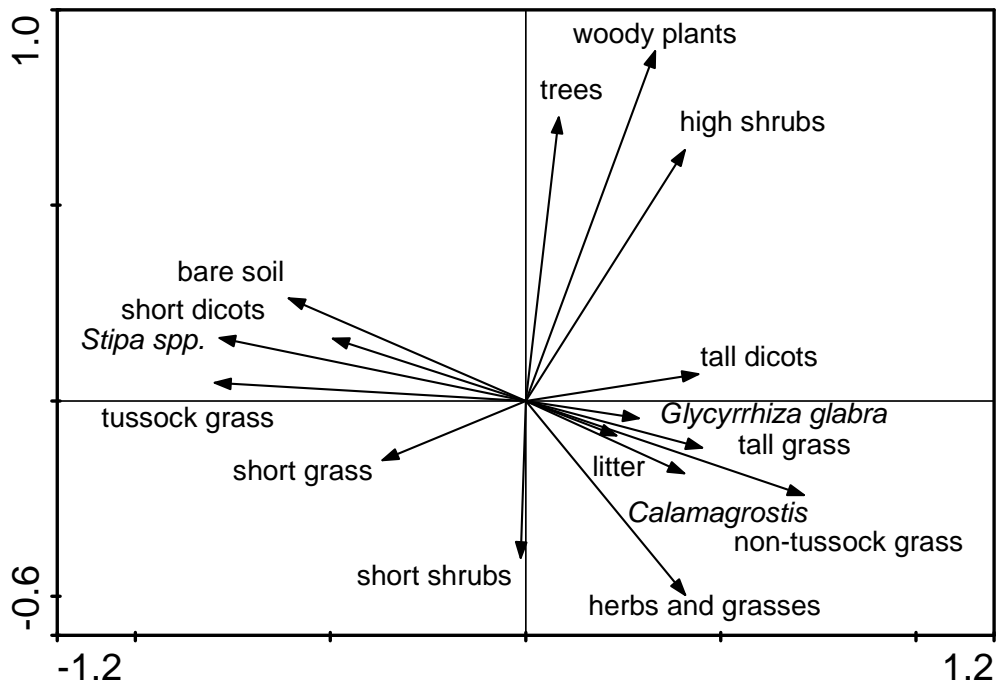


Figure 2. PCA ordination comparing habitat preferences of beetle species sampled by pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. The first ordination axis accounted for 73.2 % and first two axes for 80.5 % of the total variability (eigenvalues of first to fourth axes: 0.732; 0.073; 0.061; 0.048). All the species and samples (167) entered analysis, all the species are depicted. The first (horizontal) axis points to a gradient from species of short-turf habitats, i.e. longicorn beetles (*Dorcadion* spp.) and oil beetle *Meloe uralensis*, to tall-grassland preferring ground-beetle *Carabus hungaricus* and oil beetle *M. proscarabaeus*. The second (vertical) axis separated churchyard beetle *Blaps lethifera* and oil beetles *M. decorus* and *M. uralensis* from other species, which suggests its correlation with a gradient of bare soil extent. Note that the first axis accounted for approximately ten times more variability than the second one.

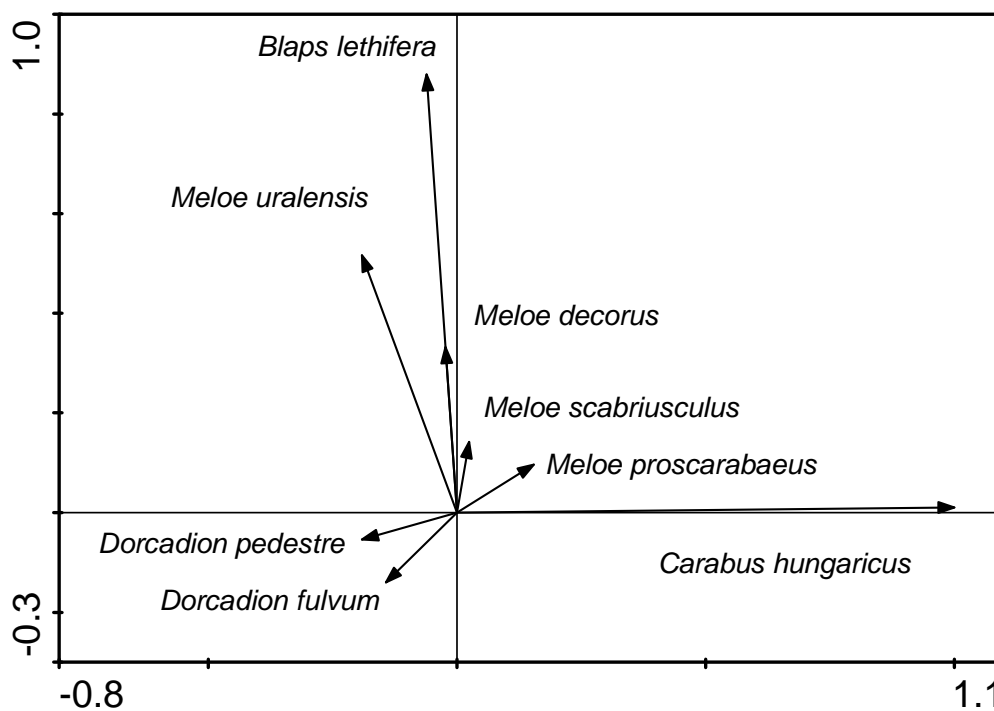
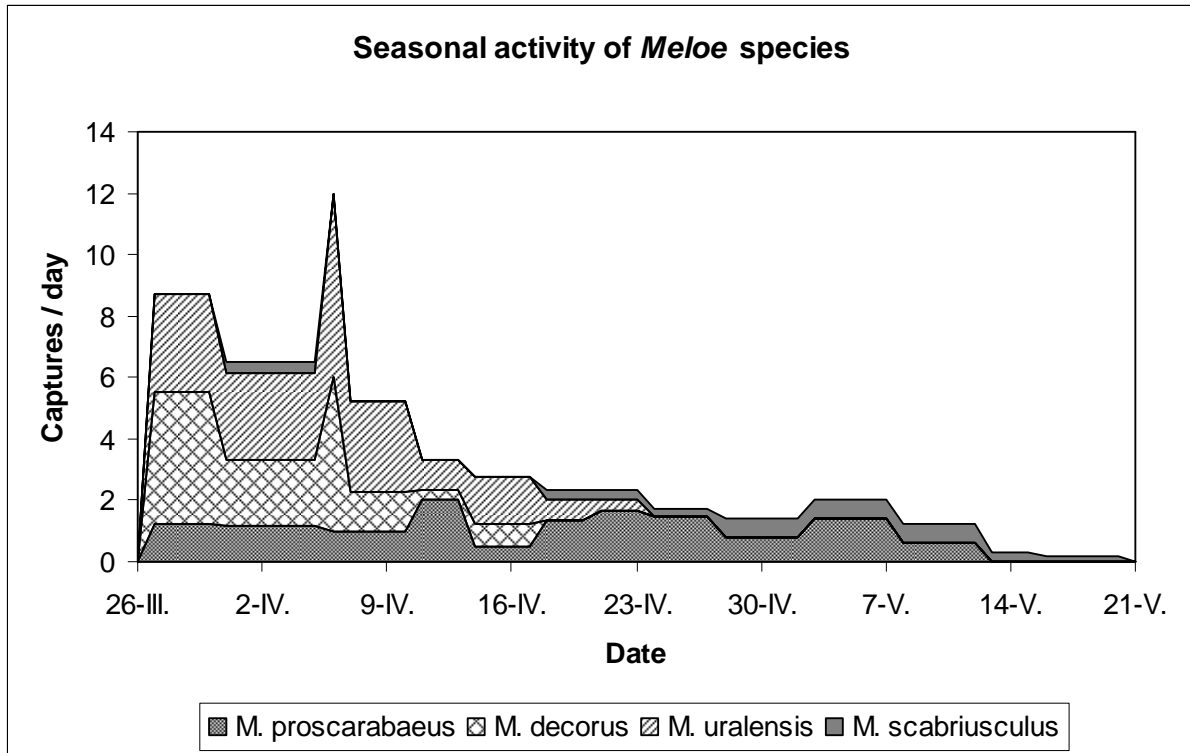


Figure 3. Seasonal changes in the numbers of four *Meloe* species caught. Captures of individual species are depicted in cumulative manner (as shaded areas) so the upper line represents total number of all species. The number of captures for each day between two controls was calculated as total number of captures in all traps in the later control date divided by number of days elapsed from the last control.



PART II

Importance of marginal habitats for grassland diversity: Fallows and overgrown tall-grass steppe as key habitats of endangered ground-beetle *Carabus hungaricus* (Coleoptera: Carabidae)

(Manuscript submitted for publication to Biological Conservation)

On April 30th under review.

Importance of marginal habitats for grassland diversity: Fallows and overgrown tall-grass steppe as key habitats of endangered ground-beetle *Carabus hungaricus* (Coleoptera: Carabidae)

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The study was carried out by three persons. I thus participated by 33%.

Abstract

Evidence-based conservation management of dry grasslands is crucial to sustain the biodiversity of these highly endangered habitats. Limited knowledge of the requirements of many groups, such as vulnerable and numerous flightless arthropods, may compromise the conservation efforts. We therefore studied the habitat selection of *Carabus hungaricus*, the globally declining, highly endangered, dry-grassland specialist listed in the EU Habitat directive, and several co-occurring beetles of conservation interest. We found that *C. hungaricus* prefers relatively humid patches of tall-grass steppe within the xeric grassland and tall-grass ruderal vegetation nearby. Females prefer drier and warmer sites than males, which may point to different habitat selection by larvae and to the need of heterogenous habitats for species survival. Other species of conservation interest, e.g. *Meloe* spp. (Coleoptera: Meloidae), *Dorcadion* spp. (Coleoptera: Cerambycidae), and/or its potential competitors, i.e. *Carabus* spp., *Calosoma* spp. (Coleoptera: Carabidae), are associated with vegetation avoided by *C. hungaricus*, such as short-grass and bare-ground patches and woody plants. Vegetation structure on medium scale (5 m) affected *C. hungaricus* abundance more than smaller and larger scales. *C. hungaricus* enters unfavoured non-forest habitats such as arable land, which allows it to spread into suitable habitats within agricultural landscapes. It strictly avoids closed forest; even narrow strips of forest thus likely act as migration barriers. The preference of *C. hungaricus* for overgrown steppe and fallow land highlights that habitats often considered of low conservation value are important to sustain grasslands biodiversity.

Abstrakt

K uchování biodiverzity stepních trávníků je nezbytný vhodně volený management těchto silně ohrožených biotopů, který se opírá o vědecké důkazy. Omezená znalost biotopových nároků mnoha skupin organismů, například velmi početných nelétavých členovců, nedovoluje úspěšnou ochranu přírody. Proto jsme studovali biotopové preference střevlíka *Carabus hungaricus*, silně ohroženého stepního druhu mizejícího v celém svém areálu, který je součástí směrnic Evropské Unie o ochraně přírody. Spolu s ním jsme se zabývali studiem biotopových preferencí několika dalších ohrožených druhů brouků. Zjistili jsme, že *C. hungaricus* preferuje relativně vlhkou vysokostébelnou stepní vegetaci. Střevlík *C. hungaricus* dále obývá vysokostébelnou ruderání vegetaci při okrajích stepi a v jejím okolí. Samice preferují sušší a teplejší biotopy než samci. To naznačuje rozdílné biotopové nároky larev ve srovnání s imagy a implikuje potřebu zachování různých biotopů pro přežití tohoto druhu. Ostatní ohrožené druhy brouků, například majky (*Meloe* spp.) (Coleoptera: Meloidae) a kozlíčci rodu *Dorcadion* (Coleoptera: Cerambycidae), a/nebo potenciální konkurenti střevlíka *C. hungaricus*, tedy střevlíci rodu *Carabus* či krajníci rodu *Calosoma* (Coleoptera: Carabidae), obývají typy vegetace, kterým se *C. hungaricus* vyhýbá. Jedná se o krákestébelnou step, plošky holé půdy a porosty dřevin. Struktura vegetace na střední prostorové škále (5 m) má silnější vliv na početnost střevlíka *C. hungaricus* než vegetace na meších a větších prostorových škálách. Střevlík *C. hungaricus* je schopen překonávat nevhodné nelesní biotopy, například pole. Tím je umožněno jeho šíření na vhodné biotopy v rámci zemědělské krajiny. Střevlík *C. hungaricus* se zásadně vyhýbá lesu. Dokonce úzký pás lesa tak pravděpodobně představuje migrační bariéru. Biotopové preference střevlíka *C. hungaricus* pro přerostlou, vysokostébelnou step a úhor ukazují, že biotopy obecně považované za málo významné z hlediska ochrany přírody jsou důležité pro uchování celkové diverzity suchých trávníků.