

Contrasting needs of grassland dwellers: habitat preferences of endangered steppe beetles (Coleoptera)

Lukas Cizek · David Hauck · Pavel Pokluda

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Abstract Temperate grasslands are local biodiversity hotspots. In Europe, their extent was mostly reduced to isolated habitat patches, whose biota is subject to extinction debt. Knowledge on requirements of dry-grassland inhabitants is thus vital to slow down decline of grassland biodiversity. We studied habitat requirements of eight flightless steppe beetles, including some of the most endangered dry-grassland specialists of the continent. The beetles were sampled using 167 pitfall traps at a pannonian dry-grassland fragment, the Pouzdrany steppe, SE Czech Republic, from March to November 2006. The number of each species captures in each trap was related to vegetation and abiotic habitat characteristics; captures of all beetles were related to each other. Two of the studied species required relatively humid microhabitats, including tall-grass steppe with litter (*Carabus hungaricus*, Carabidae) and grassland of high herb cover (*Meloe proscarabaeus*, Meloidae). Others were associated with xeric habitats (e.g. *Meloe scabriusculus*) and their early-successional stages, including short-turf vegetation (*Dorcadion fulvum*, *D. pedestre*, Cerambycidae) and/or bare-ground patches (*Blaps lethifera*, Tenebrionidae; *Meloe decorus*, *M. uralensis*). Our findings point to key importance of early-successional vegetation for grassland biodiversity, and to the fact that locally co-occurring and closely related grassland

specialists may exhibit contrasting habitat needs. Spatially and temporarily highly diversified patch management creating a fine scale mosaic of various seral stages from bare soil to tall-grass steppe is therefore the most appropriate approach for managing isolated grasslands. Prescribed burning and support of burrowing herbivores are recommended and discussed together with other measures for restoration of habitat diversity in dry-grassland fragments.

Keywords Blister beetle · Carpathian Basin · Darkling beetle · Ground beetle · Habitat selection · Longhorn beetle

Introduction

Temperate grasslands are among the most threatened biomes on the Earth; the ratio of their area converted by human activity to protected area is the highest among all the main biomes (Hoekstra et al. 2005). Agricultural intensification caused a dramatic decline in grassland extent and quality in Europe, where grasslands represent local biodiversity hotspots, rich especially in plants, invertebrates, and birds (Pons et al. 2003; Cremene et al. 2005; Pärtel et al. 2007; de Bello et al. 2010). Dry calcareous and steppic grasslands thus rank highly among priority habitats for conservation (Van Swaay 2002; WallisDeVries et al. 2002; Woodcock and Pywell 2010). Although a number of dry-grassland localities across Europe enjoy protection, the conservation efforts frequently fail to stop the decline of their biodiversity (Van Swaay and Warren 1999).

In Central Europe, the grassland deterioration culminated during the second half of the 20th century (Wittig et al. 2006; Woodcock et al. 2008). The process was rapid and intentionally hastened by government efforts

L. Cizek · P. Pokluda (✉)
Faculty of Science, University of South Bohemia, Branisovska
31, 370 05 Ceske Budejovice, Czech Republic
e-mail: pokluda.pavel@gmail.com

L. Cizek
e-mail: lukascizek@gmail.com

L. Cizek · D. Hauck · P. Pokluda
Institute of Entomology, Biology Centre ASCR, Branisovska 31,
370 05 Ceske Budejovice, Czech Republic

(Common Agricultural Policy in the Western Bloc and collectivization in the Eastern Bloc). Most productive grasslands were turned to arable land (Woodcock et al. 2008); remaining pastures and meadows suffered from increased stocking rates, artificial reseeding and heavy fertilization. Less productive grasslands, on the other hand, suffered from abandonment, often followed by spontaneous succession of woody plants or afforestation (Balmer and Erhardt 2000; Konvička et al. 2005). At protected areas, a hands-off conservation approach was applied and conservationists even hailed the invasion of woody plants as the return of reserves to their “natural state” (e.g. Veselý 2002; Möllenbeck et al. 2009). This biologically naive approach is responsible for degradation of protected grasslands in, for example, former Czechoslovakia, where the active conservation-oriented management started as late as in the 1980s (Veselý 2002). The extent of the conservation management is still insufficient at present, and dry-grassland area and quality are further deteriorating. Remaining fragments are small and isolated, their biota is declining and subject to extinction debt (Konvička et al. 2005; Wenzel et al. 2006). Numerous local extinctions have been recorded especially among species associated with habitats requiring continuous care; i.e., short-turf grasslands and bare soil (Gepp 1994; Binot et al. 1998; Beneš et al. 2002; Farkač et al. 2005). The toll is particularly high among Meloidae; out of 23 species reported for the Czech Republic, ten are considered extinct and eleven threatened with extinction (Vrabec 2005a). Populations of many endangered species are further weakened by the uniform and/or excessively intensive conservation-oriented management, often under the agri-environmental schemes (Konvička et al. 2005, 2008). Despite large expenditures, conservationists still search for measures to cope with the loss of dry-grassland biodiversity.

Conservation-efficient grassland management needs to develop an integrated approach that considers the requirements of a wide spectrum of plant and animal taxa representing various life strategies (WallisDeVries et al. 2002). However, the amount of knowledge available is greatly biased towards plants and vertebrates, especially birds (Van Wieren and Bakker 1998; Clark and May 2002). Except for butterflies and orthopterans, invertebrates are considerably less studied (Van Swaay 2002; WallisDeVries et al. 2002; Badenhausser et al. 2009; Woodcock and Pywell 2010). The information on habitat requirements is insufficient or missing for many groups, including flightless arthropods particularly vulnerable to habitat fragmentation due to their limited dispersal (Baur et al. 2005). Conservationists hence lack basic information necessary to conserve a substantial portion of dry-grassland biota.

We studied the habitat requirements of eight co-occurring flightless dry-grassland beetle species in relation to

vegetation and abiotic characteristics and to each other. The selection includes the ground-beetle *Carabus hungaricus* (Fabricius, 1792); four *Meloe* oil beetles—*M. scabriusculus* (Brandt et Erichson, 1832), *M. decorus* (Brandt et Erichson, 1832), *M. uralensis* (Pallas, 1777), and *M. proscarabaeus* (Linnaeus, 1758); the churchyard beetle *Blaps lethifera* (Marsham, 1802); and two *Dorcadion* longhorn beetles—*D. fulvum* (Scopoli, 1763) and *D. pedestre* (Poda, 1761). Most of them are endangered on the regional or global scale; *C. hungaricus* is protected under the Natura 2000 scheme. The study hopes to contribute information needed for effective conservation of dry-grassland biodiversity.

Methods

Study site and sampling

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.), located 25 km south of Brno, southern Moravia, Czech Republic. This National Nature Reserve (since 1956) 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 a regional stronghold of Pannonian biota, forming a habitat island within an intensively farmed landscape and hosting numerous threatened invertebrates and plants (e.g. Grulich 2004; Dvořák et al. 2008). Its parts are succumbing to scrub and tree regrowth following the cessation of traditional management and a hands-off conservation approach. Occasional fires and numerous European rabbits (*Oryctolagus cuniculus*) have prevented succession at 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, scattered solitary trees, scrub, and patches of sparse woodland. The steppe is surrounded by arable land, vineyards, orchards, and formerly coppiced deciduous forest (Fig. 1). The topography is rugged, the bedrock consists of Palaeogene calcareous claystone and sandstone, partly covered by Pleistocene loess. The climate is relatively warm and dry; mean annual temperature is 9.2°C, mean annual rainfall nearly 500 mm (details: Adamová 1988; Mackovčín et al. 2007).

An extensive capture-and-release pitfall trapping survey, aimed mainly on monitoring the EU protected *Carabus hungaricus*, was carried out at the steppe in 2006 (Pokluda et al. in press). A total of 167 pitfall traps were distributed to all grassland habitat types existing at the steppe and in

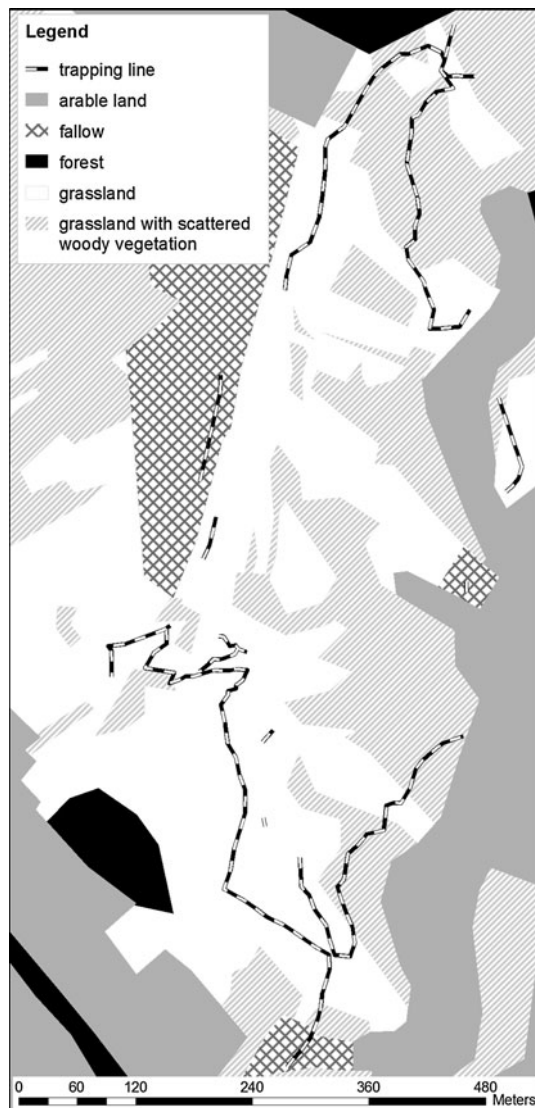


Fig. 1 Map of the Pouzdrany steppe and its vicinity, Czech Republic, showing distribution of major vegetation types and pitfall traps

its vicinity (Fig. 1). The traps were distributed at various distances (distance between neighboring traps—mean: 19.24 m; SD: 20.49; min: 5 m). The habitats and vegetation types covered were: 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 (the steppe was covered by snow until a few days before activation of the traps, and the first snow fell just after their removal). Traps were inspected 1–2 times a week, summing 45 inspections in total. Captures of the eight beetle species (see below and Table 1), the trap number, and the inspection date were recorded. Data on surrounding vegetation were recorded by an experienced botanist. Beetles were released 2 m from the respective trap.

Study species

The selected ground-dwelling grassland beetles are easily identifiable in the field and were commonly found (total $n > 15$, see Table 1) in the traps. The selection comprises eight species belonging to four genera and four families:

- i. The ground-beetle *Carabus (Pachystus) hungaricus* (Carabidae) inhabits dry calcareous, loess, and sand grasslands from lowlands up to nearly 600 m a.s.l. in the Carpathian Basin (Hürka 1996; Bérces et al. 2008). The species is globally declining, protected and/or red-listed in most countries of occurrence, listed also in Annexes II and IV of the EU Habitats Directive (Borodin et al. 1984; Shcherbak 1994; Arndt and Trautner 2004; Veselý et al. 2005; Bérces et al. 2008). Its habitat preferences are described in detail by Pokluda et al. (in press). In this paper, habitat needs of *C. hungaricus* are presented to illustrate the variability in habitat use by dry-grassland beetles.
- ii. The oil beetles of genus *Meloe* (Meloidae) parasitize bees (superfamily Apoidea) in preimaginal stages, whereas adults are herbivorous. Females oviposit in chambers dug in the ground, the first instar larvae, called triungulins, disperse and attach to bees which carry them to their nests (Hafernik and Saul-Gershenz 2000; Lückmann and Niehuis, 2009). Triungulins of subgenus *Micromeloe* (see below) are assumed not to be phoretic, and find the host nests on their own (Vrabec et al. 2001; di Giulio et al. 2002; Lückmann and Scharf 2004; Lückmann 2005; but see Vrabec 2005b) suggesting their low mobility and closer association between distribution of *Micromeloe* adults and host nests. The assumption of non-phoretic triungulins, however, seems contradicted by the rapid spread of *Micromeloe decorus* to distant and isolated sites (Vrabec 1993, 2002). Oil beetles have experienced a dramatic decline in Central Europe and are among the most threatened insects there (Vrabec 2005a; Lückmann and Niehuis 2009). Four species of the genus were studied:

M. (Eurymeloe) scabriusculus is distributed from France to Central Asia. Adults occur mainly in April and May. The bee *Andrena vaga* (Panzer, 1799) is considered a potential host (Fellendorf et al. 2004). Bologna (1991) lists the species as mesophilous, occasionally exploiting woody habitats; other authors suggest that it requires xero-thermophilous, open-habitats. In Central Europe it is distributed in lower elevations (Stebnicka 1987; Švihla 1996; Dvořák and Vrabec 2007; Lückmann and Niehuis 2009).

M. (Micromeloe) decorus is distributed from eastern France to Central Asia, known in all countries of Central Europe. Adults occur from February until May with their

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

Beetle species	n	CS ^a
Ground beetles (Carabidae)		
<i>Carabus hungaricus</i> (Fabricius, 1792)	3,819	VU
Oil beetles (Meloidae)		
<i>Meloe scabriusculus</i> (Brandt et Erichson, 1832)	16	NT
<i>Meloe decorus</i> (Brandt et Erichson, 1832)	44	
<i>Meloe uralensis</i> (Pallas, 1777)	60	CR
<i>Meloe proscarabaeus</i> (Linnaeus, 1758)	54	EN
Darkling beetles (Tenebrionidae)		
<i>Blaps lethifera</i> (Marsham, 1802)	100	
Longhorn beetles (Cerambycidae)		
<i>Dorcadion fulvum</i> (Scopoli, 1763)	25	D
<i>Dorcadion pedestre</i> (Poda, 1761)	25	D

^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)

peak in March and April. *Andrena flavipes* (Panzer, 1798) and *A. vaga* (Panzer, 1799) are considered its potential hosts. It is a thermophilous species of lower elevations (Stebnicka 1987; Bologna 1991; Švihla 1996; Dvořák and Vrabec 2007; Lückmann and Niehuis 2009).

M. (Micromeloe) uralensis is distributed from the Pannonian region to Central Asia (Dvořák 1983; Dvořák and Vrabec 2007). Adults occur from April until May (Švihla 1996). It is critically endangered in the Czech Republic (Vrabec 2005a), recently known from several sites that include loess or limestone steppe fragments, vineyards, orchards, and arable field margins (M. Holomčík, pers. comm.; S. Krejčík, pers. comm.; M. Škorpík, pers. comm.). To our knowledge, the host species are unknown; information on habitat selection by adults consists of vague reports, e.g. steppes or “xero-thermophilous species” (Švihla 1996).

M. (Meloe) proscarabaeus is a Eurosiberian species widely distributed in Europe. Adults occur from February until July with their peak from March until May. Although still considered one of the most widespread Meloidae species in Central Europe, *M. proscarabaeus* declined dramatically during the 20th century. Its host species include plasterer bees (genus *Colletes*, Latreille, 1802), *Anthophora retusa* (Linnaeus, 1758), *Andrena carantonica* (Pérez, 1992), and *A. haemorrhoea* (Fabricius, 1781); potential hosts include *Andrena flavipes* (Panzer, 1798), *A. nitida* (Müller, 1776), and *A. vaga* (Panzer, 1799). The species inhabits grasslands and forest edges from lowlands to mid elevations (Stebnicka 1987; Knight 1995; Švihla 1996; Vrabec 2006; Lückmann and Niehuis 2009).

iii. The churchyard beetle *Blaps lethifera* (Tenebrionidae) is taxonomically a difficult species. Central-European taxa of *B. lethifera* species group are considered synonyms of *B. lethifera* (Šustek 1982; Novák 2007). This Palearctic species is widely

distributed in Europe, reaching North Africa, Asia Minor, and Central Asia (Picka 1978; Ferrer and Picka 1990; Vsevolodova-Perel' and Sizemskaya 2007). Feeding on dead plant matter, it occupies rodent burrows in mesophilic- to desert-steppes, but also human settlements (Picka 1978; Nagumanova 2007; Vsevolodova-Perel' and Sizemskaya 2007).

iv. The longhorn beetles *Dorcadion (Carinatodorcadion) fulvum* and *D. (Cribridorcadion) pedestre* (Cerambycidae) are distributed in Central and south-eastern Europe (Sama 2002). In the Czech Republic, *D. fulvum* is most abundant on relatively humid meadows and pastures of lower elevations, but occupies also drier habitats. *D. pedestre* inhabits steppes, pastures, and other grasslands of lower elevations (Sláma 1998). Larvae of both species develop in the soil, feeding on roots of herbs and/or grasses (Sláma 1998; Sama 2002). Both species experienced a marked decline in the former Czechoslovakia during the 20th century (cf. Sláma 1998).

Variables

The *response variables* were the numbers of captures of the eight beetle species (see Table 1) per trap for the entire study period. In addition, the following vegetation and abiotic variables were recorded:

Vegetation: Percent covers of the following vegetation characteristics and selected indicative or otherwise noteworthy plants were estimated on two spatial scales (0.5 and 2.5 m, within circles of the respective radius with trap in the centre): (i) bare soil; (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.

Abiotic: (i) temperature; (ii) humidity; (iii) soil reaction; (iv) soil nitrogen content; (v) light. Values of all variables were estimated using plant-species data from plot around each trap (circle, 0.5 m radius). 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 and 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 are relative, ranging from 1 to 9 for all variables except for the humidity (1–12). The higher the Borhidi value, the higher the value of a given characteristic; the values for dry-grassland types of the region, including the study site, are given in Dúbravková et al. (2010). 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 and Witte (2004).

Analyses

Using regression and multivariate analyses, we investigated effects of vegetation and abiotic variables on the number of captures of the given beetle species, and compared habitat preferences of the sampled beetle species. In all analyses, traps represented samples characterized by the number of captures of the sampled beetle species, surrounding vegetation, and abiotic factors; the vegetation variables were log-transformed.

The effects of vegetation and abiotic variables on the number of captures of individual beetle species were investigated using Generalized Linear Models (GLM, quasipoisson distribution of residual variability, log link function). For each beetle species, full models with the vegetation variables on the two spatial scales (0.5 and 2.5 m) were separately fitted and then compared using the model deviance information (=explained variability) and Mallows' Cp statistic. The vegetation variables on the spatial scale with the higher explanatory power for the given beetle species together with the abiotic variables entered further analyses. Full model investigating effect of all variables on the number of captures of the given beetle species was then fitted and tested using *F*-test. If the full model was significant, independent (marginal) effects of individual variables on the number of captures of the given beetle species were assessed using *F*-test.

The relations among individual explanatory variables were investigated using an unconstrained linear ordination, the principal component analysis (PCA). Scaling focused on inter-species correlations, species scores were divided by standard deviations, species data were centered, samples were neither centered nor standardized.

Distribution of all the beetle species in relation to each other was investigated using an unconstrained linear ordination, the principal component analysis (PCA). Data 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 (Maindonald and Braun 2003) and multivariate analyses using Canoco for Windows 4.5 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003).

Results

In total, 4,143 captures of the eight studied beetle species were recorded (for numbers of captures see Table 1). *Blaps lethifera* and *Carabus hungaricus* occurred continually from the spring until the beginning of October and November, respectively. Adults of *Meloe decorus*, *M. uralensis*, and *M. proscarabaeus* occurred from the beginning of the sampling (i.e. late March) until April 17, April 23, and May 12, respectively. *M. scabriusculus* occurred between the beginning of April and May 20. *Dorcadion fulvum* occurred from the middle of May until early July, with maximum activity between the middle of May and the middle of June. *D. pedestre* occurred from the third third of April until the second third of June with maximum activity in May.

Full models with the vegetation variables on 2.5 m scale exhibited higher explanatory power than 0.5 m scale for all beetles, except for *M. proscarabaeus* which exhibited opposite pattern. The studied variables affected distribution of each beetle species as the full models investigating the effect of all variables on number of captures of individual species were significant (Table 2). GLM revealed following relations between studied beetles and environmental variables:

Carabus hungaricus captures were positively affected by litter, wood small-reed, tall grass, herbs and grasses, tall dicots, humidity, and soil nitrogen content and negatively affected by feather grasses, short dicots, tussock grass, trees, bare soil, temperature, soil reaction, and light.

Meloe scabriusculus captures were positively influenced by soil reaction and negatively influenced by high shrubs. *M. decorus* captures were positively affected by soil reaction. *M. uralensis* captures were positively influenced

Table 2 Full models of effect of vegetation and abiotic variables on number of beetle captures at pitfall traps on the Pouzdrany steppe, Czech Republic (GLM, quasipoisson distribution of residual variability, log link function, $n = 167$) tested using F -tests

Model	df	Residual deviance	Model deviance	F	P
<i>Carabus hungaricus</i> 2.5 m					
Null	166	2920.5			
Full	22,144	1003.5	1917.0	12.13	*****
<i>Meloe scabriusculus</i> 2.5 m					
Null	166	77.8			
Full	22,144	34.2	43.6	4.04	*****
<i>Meloe decorus</i> 2.5 m					
Null	166	152.7			
Full	22,144	98.9	53.9	2.69	***
<i>Meloe uralensis</i> 2.5 m					
Null	166	225.6			
Full	22,144	133.8	91.8	2.67	***
<i>Meloe proscarabaeus</i> 0.5 m					
Null	166	280.0			
Full	22,144	126.5	153.6	3.25	****
<i>Blaps lethifera</i> 2.5 m					
Null	166	244.5			
Full	22,144	177.2	67.3	2.21	**
<i>Dorcadion fulvum</i> 2.5 m					
Null	166	123.7			
Full	22,144	55.9	67.9	4.54	*****
<i>Dorcadion pedestre</i> 0.5 m					
Null	166	173.3			
Full	22,144	27.8	145.5	3.25	****

The vegetation characteristics of trap surroundings (within a circle of 0.5 or 2.5 m radius) and the abiotic characteristics of trap surroundings (circle of 0.5 m) were explanatory variables. The spatial scales of vegetation variables 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 0.5 and 2.5 m scales

** $P < 0.01$; *** $P < 0.001$;
**** $P < 0.0001$; *****
 $P < 0.00001$

by short dicots, feather grasses, temperature, and soil reaction and negatively influenced by wood small-reed and humidity. *M. proscarabaeus* captures were positively affected by tall dicots, broad-leaved herbs, and soil nitrogen content and negatively affected by tussock grass and soil reaction.

Blaps lethifera captures were positively influenced by extent of bare soil and negatively influenced by covers of herbs and grasses and tall grass.

Dorcadion fulvum captures were negatively affected by high shrubs. *D. pedestre* captures were positively affected by broad-leaved herbs, short dicots, and short grass and negatively affected by tall grass and litter (see Table 3 for details for all species, including variables with marginally significant effects ($0.05 > P > 0.01$) not mentioned above).

The PCA ordination investigating the relations among individual vegetation and abiotic characteristics distinctly separated three groups of variables (Fig. 2). The first (horizontal) axis separated variables indicating xero-thermophilous vegetation with bare soil, including short turf and feather grasses, from variables indicating relatively humid tall-grass steppe with high herb cover and litter, partly degraded by invasive plants. The second (vertical)

axis separated woody plant variables. The first axis thus describes a gradient from xeric short-grass steppe with bare soil to relatively humid tall-grass steppe with high herb cover, whereas the second axis represents a gradient from short to high woody plants. The 2.5 m scale of vegetation variables was selected for illustration since it had better explanatory power for majority of the studied beetles in GLM (see above). All the abiotic characteristics are affected by topography and vegetation and thus strongly correlated (Cornwell and Grubb 2003; Chytry et al. 2009). Thicker vegetation (occurring mostly on flat sites and in depressions) slows down evaporation, lowers solar radiation, and contributes to higher nutrient content. Such sites then host fewer xerophilous plants, which in turn indicates lower temperature. Higher pH indicates drier and warmer sites due to calcium washing from more humid sites and/or the fact, that xerothermophilous plants are mostly calcicolous (Chytry et al. 2007).

In the PCA ordination comparing habitat preferences of the studied beetles, the first (horizontal) axis separated *D. fulvum*, *D. pedestre*, and *M. uralensis* from *C. hungaricus* and *M. proscarabaeus* (Fig. 3). The second (vertical) axis separated *B. lethifera*, *M. decorus*, and *M. uralensis* from other species. The first axis accounted for approximately ten

Table 3 Effect of vegetation and abiotic variables on grassland beetles on the Pouzdrany steppe, Czech Republic. Independent (marginal) effects of the abiotic and the vegetation characteristics of trap surroundings (within a circle of 0.5 or 2.5 m radius) on the

number of captures of individual species at pitfall traps, as returned by *F*-test (GLM, quasipoisson distribution of residual variability, log link function, n = 167)

Model	Regression coefficient b	df	Residual deviance	Model deviance	F	P
<i>Carabus hungaricus</i> 2.5 m						
Null		166	2920.5			
Temperature	−1.67	1,165	1968.0	952.5	72.75	*****
Soil reaction	−1.29	1,165	2265.8	654.7	38.27	*****
Humidity	0.88	1,165	2338.3	582.3	35.79	*****
<i>Stipa</i> spp.	−0.30	1,165	2428.1	492.5	29.33	*****
Soil nitrogen content	0.44	1,165	2466.0	454.5	25.47	*****
Litter	1.79	1,165	2498.3	422.2	22.58	*****
<i>Calamagrostis epigejos</i>	0.23	1,165	2563.3	357.2	18.28	****
Light	−1.01	1,165	2593.5	327.1	17.98	****
Short dicots	−0.37	1,165	2570.7	349.8	17.33	****
Bare soil	−0.48	1,165	2591.3	329.3	15.94	****
Tall grass	0.49	1,165	2618.2	302.3	14.07	***
Herbs and grasses	0.95	1,165	2652.1	268.4	12.16	***
Tussock grass	−0.20	1,165	2704.7	215.9	9.80	**
Trees	−0.30	1,165	2736.8	183.7	8.56	**
Tall dicots	0.22	1,165	2759.7	160.9	7.61	**
<i>Glycyrrhiza glabra</i>	−0.39	1,165	2811.9	108.6	4.89	*
<i>Meloe scabriusculus</i> 2.5 m						
Null		166	77.8			
Soil reaction	3.20	1,165	70.0	7.9	8.32	**
High shrubs	−1.69	1,165	71.5	6.4	7.48	**
Light	2.26	1,165	73.0	4.8	5.04	*
<i>Meloe decorus</i> 2.5 m						
Null		166	152.7			
Soil reaction	1.88	1,165	144.2	8.5	6.92	**
Tussock grass	0.41	1,165	145.5	7.2	5.76	*
Light	1.52	1,165	146.6	6.2	4.78	*
Non-tussock grass	−0.29	1,165	146.9	5.9	4.65	*
Short grass	0.33	1,165	146.9	5.9	4.63	*
Tall grass	−0.54	1,165	146.9	5.8	4.62	*
<i>Meloe uralensis</i> 2.5 m						
Null		166	225.6			
Short dicots	0.57	1,165	198.3	27.3	15.17	***
Temperature	2.48	1,165	197.4	28.2	13.28	***
Humidity	−1.86	1,165	202.1	23.6	11.72	***
<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	**
Soil reaction	2.24	1,165	209.7	15.9	7.46	**
Soil nitrogen content	−0.98	1,165	211.3	14.3	6.62	*
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	*
<i>Meloe proscarabaeus</i> 0.5 m						
Null		166	280.0			
Soil nitrogen content	1.19	1,165	205.1	75.0	33.42	*****

Table 3 continued

Model	Regression coefficient b	df	Residual deviance	Model deviance	F	P
Tussock grass	−0.66	1,165	243.3	36.7	10.58	**
Soil reaction	−2.15	1,165	242.7	37.3	8.76	**
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	**
Humidity	1.65	1,165	247.2	32.8	6.40	*
<i>Blaps lethifera</i> 2.5 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> 2.5 m						
Null		166	123.7			
High shrubs	−166.69	1,165	102.4	21.3	17.84	****
Humidity	−1.92	1,165	113.3	10.4	6.44	*
Short grass	0.57	1,165	113.9	9.8	6.09	*
Tussock grass	0.70	1,165	114.1	9.6	5.84	*
Soil nitrogen content	−1.55	1,165	112.3	11.4	5.55	*
<i>Calamagrostis epigejos</i>	−1.15	1,165	115.5	8.3	5.17	*
<i>Dorcadion pedestre</i> 0.5 m						
Null		166	173.3			
Tall grass	−1.49	1,165	95.5	77.8	45.58	*****
Broad-leaved herbs	2.27	1,165	126.0	47.3	15.77	***
Litter	−4.66	1,165	143.2	30.1	8.03	**
Short dicots	0.84	1,165	138.9	34.4	7.87	**
Short grass	0.79	1,165	148.9	24.4	6.83	**
Soil nitrogen content	−2.33	1,165	153.5	19.8	5.51	*

The spatial scales of vegetation variables 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 0.5 and 2.5 m scales. Only significant results are shown

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ***** $P < 0.00001$

times more variability than the second one. As revealed by analyses of individual species requirements (see above), the first axis separated species of short-turf habitats from inhabitants of tall grasslands, and the second axis separated species dependent on bare soil. The first axis thus describes a gradient from short- to tall-grass vegetation, whereas the second axis represents a gradient of bare soil extent.

Discussion

Habitat preferences

The studied beetles co-occurring within a single dry-grassland locality varied and partly contrasted in habitat use. Two species required relatively humid microhabitats, including tall-grass steppe with litter (*Carabus hungaricus*,

Carabidae) and grassland with a high herb cover (*Meloe proscarabaeus*, Meloidae). Others were associated with xeric habitats (e.g. *Meloe scabriusculus*) and their early seral stages such as short-turf vegetation (*Dorcadion fulvum*, *D. pedestre*, Cerambycidae; *Meloe decorus*) and/or bare-soil patches (*Blaps lethifera*, Tenebrionidae; *Meloe uralensis*).

The ground-beetle *C. hungaricus* preferred taller steppe vegetation with high herb cover and litter in relatively humid parts of the steppe, as well as in patches of taller non-woody vegetation at steppe margins, including fallows and field edges. Its habitat use is discussed in detail by Pokluda et al. (in press).

The diversity of habitat requirements is well illustrated on the four *Meloe* species. Avoidance of shrubs and preference for light and higher pH indicate that *M. scabriusculus* is a species of open xerophilous habitats

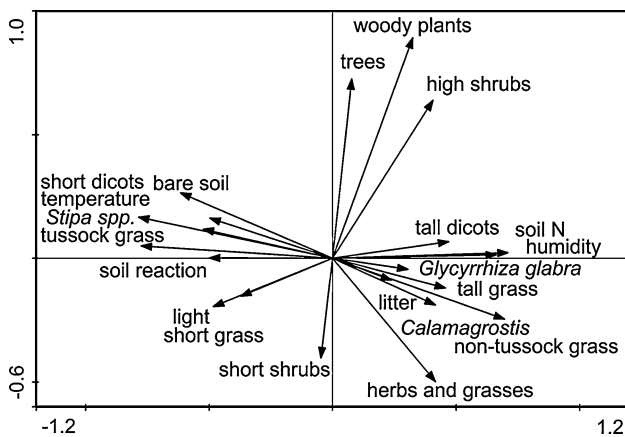


Fig. 2 PCA ordination comparing relations among the vegetation and the abiotic characteristics of trap surroundings on the Pouzdrany steppe, Czech Republic. The first ordination axis accounted for 27.2% and first two axes for 42.6% of the total variability (eigenvalues of first to fourth axes: 0.272; 0.154; 0.110; 0.103). All the variables and samples (167) entered analysis, variables with minimum fit = 6 are depicted. A clear separation of variables indicating xero-thermophilous short-turf steppe with bare soil patches or *Stipa* spp. growths (i.e., tall-grass vegetation with numerous bare soil patches) from variables indicating relatively humid tall-grass steppe with high herb cover and litter, partly degraded by invasive plants (*horizontal axis*), and woody plant variables (*vertical axis*) is apparent. The vegetation variables were estimated within a circle of 2.5 m radius and the abiotic variables within a circle of 0.5 m radius

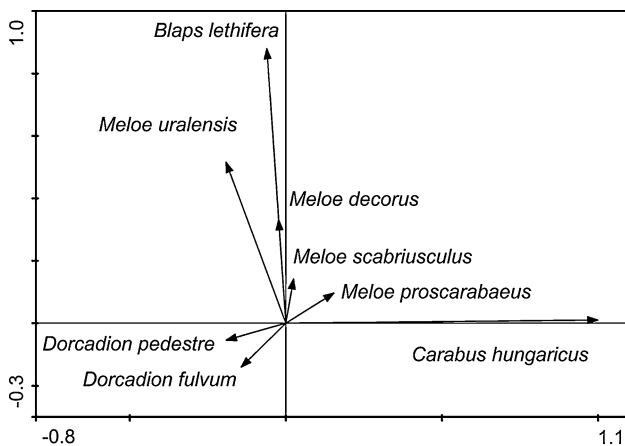


Fig. 3 PCA ordination comparing habitat preferences of beetle species sampled by pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. The first ordination axis accounted for 73.2% and first two axes for 80.5% of the total variability (eigenvalues of first to fourth axes: 0.732; 0.073; 0.061; 0.048). All the species and samples (167) entered the analysis, all the species are depicted. The first (*horizontal axis*) points to a gradient from species of short-turf habitats, i.e. longhorns of genus *Dorcadion* 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

(in agreement with Stebnicka 1987; Švihla 1996; Lückmann and Niehuis 2009; but see Bologna 1991). *M. decorus* and *M. uralensis* require xeric, mostly short-turf vegetation with bare soil patches, while avoiding tall and non-tussock grasses. *M. uralensis* preference for feather grasses (i.e., xerophilous tussock tall grass with patches of bare soil) indicates that vegetation height is less relevant for the species if bare soil is present. Although the analyses did not exhibit *M. decorus* dependence on bare soil directly, positive effects of short and tussock grass (i.e. vegetation with large bare-soil extent) on its distribution suggest the species does require bare soil. *M. proscarabaeus* prefers high herb cover on relatively humid sites, or the least xeric conditions of all the *Meloe* species studied. This may explain why *M. proscarabaeus* remains one of the most common Meloidae of the continent (Lückmann and Niehuis 2009), as mesic grasslands with high herb cover remain relatively abundant across Europe. The habitat selection of *Meloe* beetles is determined by the distribution of resources including adult food plants, bare soil patches for oviposition, flowers visited by the host bees, and their nests. To attribute the distribution of studied *Meloe* species to that of their hosts is difficult as individual *Meloe* species either exploit a wide range of host bees, and/or the hosts are not sufficiently known (Lückmann and Niehuis 2009). Further studies of *Meloe* hosts are needed for more efficient conservation.

The churchyard beetle *B. lethifera* exhibits a strong preference for bare soil and avoids overgrowing, degraded steppe. Effect of no abiotic characteristic was detected, possibly owing to the fact that *B. lethifera* often occupies mammal burrows (Picka 1978), where conditions are rather independent from the surface. Furthermore, burrow entrances are usually surrounded by bare soil and short-turf vegetation. The studied population of *B. lethifera*, however, hardly depends solely on burrows unless it exploits burrows of small rodents, e.g. voles (*Microtus* spp.), as only a few burrows of larger mammals remain at the study site after the local disappearance of rabbits and European ground squirrels (*Spermophilus citellus*).

The longhorn beetles *D. pedestre* and *D. fulvum* both prefer short-turf vegetation at drier sites with lower soil nitrogen. *D. fulvum* prefers also tussock grasses. Sláma (1998) considers *D. fulvum* more mesophilous than *D. pedestre*. The detected *D. fulvum* preference for abiotic factors might be biased by absence of relatively humid short-turf conditions at the study site, as more humid parts of the reserve are covered by taller, dense vegetation, resulting from spontaneous succession. This would correspond to habitat requirements of *D. fuliginator*, that prefers light-exposed and warm conditions, but with relatively large ranges in humidity and nutrient content (Baur et al. 2002).

Management recommendations

As the habitat needs of the studied species illustrate, short-turf and bare-soil conditions are essential to sustain dry-grasslands biota. The early-successional habitats, however, currently cover only a small part of the study site, persisting at its driest and the most trampled parts and near mammal burrows. Shrinking of the early-successional patches is a general problem of European grassland biota (e.g. Thomas et al. 1994; Schaub et al. 2010). The problem, however, is not adequately addressed in Central Europe, as the decline and numerous local extinctions of fauna associated with short-turf and bare-soil conditions illustrate (Beneš et al. 2002; Farkač et al. 2005; Holuša and Kočárek 2005; Straka 2005; Hulová and Sedláček 2008; Lückmann and Niehuis 2009). Restoration of the early-successional habitats is hence vital at the study site and other grassland reserves, and the management recommendations discussed below are of a wider relevance.

Patches of early-successional conditions should be restored at both the driest and more humid parts of the reserve, including the parts currently overgrown by woody plants. Grazing, trampling, prescribed burning, sod cutting, and support of local populations of burrowing mammals are among the available measures (Pykälä 2000; Stewart and Pullin 2008). Although often regarded detrimental to grassland diversity (Andersen 1995; Bell et al. 2001; Vickery et al. 2001; Torre et al. 2007), trampling creates bare-soil patches sustaining endangered dry-grassland biota (Schläpfer et al. 1998; Samways and Kreuzinger 2001; Wirtitsch et al. 2001; Atkinson et al. 2004; Schaub et al. 2010). Colonial, burrowing mammal herbivores (e.g. rabbits, ground-squirrels) create a fine vegetation mosaic with bare-soil patches (Thomas and Jones 1993; Winter et al. 2002; Davies et al. 2005; Brereton et al. 2008; Read et al. 2008); their support is thus a highly efficient management tool. Compared to other measures, prescribed burning is highly effective tool in suppressing woody plants; it is cost-efficient and suitable if there is no immediate threat of invasion by fire-tolerant plants (Borkowski 2004; Möllenbeck et al. 2009). Except for grazing, however, the above measures are rarely applied to protected dry grasslands of Central Europe; where grass mowing remains the most commonly used approach. Although better than no management, mowing results in rather uniform turf height and closure of vegetation cover (Harper 2007). To prevent this, it should always be applied in a mosaic manner, accompanied by measures facilitating for soil disturbances (e.g. Gregory and Wright 2005).

It should be kept in mind, however, that the current dry-grassland remnants often sustain, aside from early-successional species, also species associated with later-successional stages, such as tall-grass steppe and scattered

woody vegetation. Their needs have to be also accommodated; native woody plants thus should be removed selectively and a proportion of each grassland site should be periodically left unmanaged to accommodate later grassland seral stages. This makes management of isolated dry grasslands particularly challenging (Balmer and Erhardt 2000; Bourn and Thomas 2002; WallisDeVries et al. 2002).

The contrasting habitat requirements of the studied beetles present further evidence that the spatially and temporarily diversified, rotational patch management is the most appropriate approach to preserve the diverse conditions and high local biodiversity (Balmer and Erhardt 2000; WallisDeVries and Raemakers 2001; WallisDeVries et al. 2002; Pöyry et al. 2004; Saarinen and Jantunen 2005; Schmidt et al. 2008).

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