Insect Conservation and Diversity

Insect Conservation and Diversity (2012) **5,** 27–36 doi: 10.1111/j.1752-4598.2011.00146.x

Importance of marginal habitats for grassland diversity: fallows and overgrown tall-grass steppe as key habitats of endangered ground-beetle *Carabus hungaricus*

PAVEL POKLUDA,[1,2] DAVID HAUCK[1] and LUKAS CIZEK[1,2] [1]Biology Centre ASCR, Institute of Entomology, Ceske Budejovice, Czech Republic and [2]Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

Abstract. 1. To facilitate effective conservation management of dry-grassland diversity we studied the habitat selection of *Carabus hungaricus*, the globally declining, highly endangered, dry-grassland specialist beetle listed in the EU Habitats Directive, and several co-occurring beetles at a pannonian dry-grassland fragment, the Pouzdrany steppe, SE Czech Republic. The beetles were sampled using 186 pitfall traps from March to November 2006. Number of *C. hungaricus* captures in each trap was related to vegetation and abiotic habitat characteristics; captures of all sampled beetles in each trap were related to each other.

2. We found that *C. hungaricus* prefers relatively humid patches of tall-grass steppe within the xeric grassland and tall-grass ruderal vegetation nearby. During the breeding period, females preferred drier and warmer sites than males.

3. Its potential competitors, i.e., *Carabus* spp., *Calosoma* spp. (Coleoptera: Carabidae), and other species of conservation interest, including *Meloe* spp. (Coleoptera: Meloidae), *Dorcadion* spp. (Coleoptera: Cerambycidae), were associated with vegetation avoided by *C. hungaricus*, such as short-grass and bare-soil patches and woody plants.

4. Vegetation structure within 2.5 m affected *C. hungaricus* captures more than on smaller and larger scales. *Carabus 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.

5. The preference of *C. hungaricus* for overgrown steppe and fallow land highlights that habitats often considered of low conservation value are important to sustain grassland biodiversity.

Key words. Blaps, Carpathian Basin, continental grassland, longhorn beetle, Natura 2000, oil beetle, sex-dependent habitat selection.

Introduction

Temperate grasslands rank among the most threatened biomes on Earth (Hoekstra *et al*., 2005). This applies also for Europe, where grasslands have declined dramatically in extent and quality due to agricultural intensification or abandonment (Cremene *et al*., 2005; de Bello *et al*., 2010). In Eastern Central Europe, grasslands declined most during the communist-era agriculture collectivisation, when their acreage locally decreased to less than half its previous extent within just two decades (Skaloš, 2006). Productive areas of lowlands were hit particularly hard (e.g., Skaloš, 2006); most such grasslands were turned to arable land,

Correspondence: Lukas Cizek, Biology Centre ASCR, Institute of Entomology, Branisovska 31, CZ-370 05 Ceske Budejovice, Czech Republic. E-mail: lukascizek@gmail.com

© 2011 The Authors
Insect Conservation and Diversity © 2011 The Royal Entomological Society

or abandoned and afforested (Woodcock *et al*., 2008). To make matters worse, a hands-off conservation approach was frequently applied to the protected sites; conservationists often hailed the invasion of woody plants as the return of grasslands to their "natural" state (e.g., Veselý, 2002).

Dry or steppic grasslands are considered regional biodiversity hotspots (Cremene *et al*., 2005). In Central Europe, they have been drastically affected by agricultural intensification. Charismatic steppe vertebrates such as the great bustard (*Otis tarda*) and the European ground squirrel (*Spermophilus citellus*) are highly threatened (Hulová & Sedláček, 2008; Alonso *et al*., 2009) whilst numerous local extinctions have been documented among invertebrates (Gepp, 1994; Binot *et al*., 1998; Farkač *et al*., 2005). In the Czech Republic, active management of protected grasslands started as late as in the 1980s (Veselý, 2002), and its measures are still insufficient. In parallel, too intensive reserve management may cause homogenisation and other adverse effects (Konvička *et al*., 2008; Marini *et al*., 2009). Conservation-efficient grassland management needs to acknowledge the requirements of the wide spectrum of endangered grassland inhabitants. Despite the growing body of knowledge on requirements of such taxa as birds and butterflies, data on many groups, including numerous and highly vulnerable flightless arthropods, are scarce or missing (Leather *et al*., 2008).

As a typical steppe species, the ground-beetle *Carabus hungaricus* (Fabricius, 1792) represents Pannonian steppe invertebrates in EU legislation. Its fate mirrors the recent history of its habitat. The species is declining throughout its range and is near extinction in many regions (Borodin *et al*., 1984; Arndt & Trautner, 2004; Bérces *et al*., 2008). Its basic biology remains poorly known. To strengthen the information base for effective conservation of grassland diversity, we carried out a detailed survey on habitat selection of this highly endangered species, and compared its habitat preferences to that of other threatened flightless grassland beetles, such as oil beetles (*Meloe* spp.), churchyard beetle (*Blaps lethifera*), and longhorn beetles (*Dorcadion* spp.).

Our study investigated: (i) effect of vegetation characteristics on *C. hungaricus* captures at three different spatial scales, (ii) effect of abiotic characteristics on *C. hungaricus* captures, (iii) sex-dependent patterns in habitat selection of *C. hungaricus*, and (iv) habitat selection of *C. hungaricus* in relation to its co-occurring potential competitors and/or grassland specialists of conservation interest.

Materials and methods

Study species

Carabus (*Pachystus*) *hungaricus* (Fabricius, 1792) is a polytypic species distributed from Central Europe to Eastern Siberia (Bousquet *et al*., 2003), or confined only to Europe, depending on the status of its easternmost subspecies (Turin *et al*., 2003). The nominotypic subspecies, *C. hungaricus hungaricus* is restricted to the Carpathian Basin and Bulgaria (Guéorguiev & Guéorguiev, 1995; Bousquet *et al*., 2003; Turin *et al*., 2003; Bérces *et al*., 2008).

This thermophilous beetle inhabits dry calcareous, loess, and sand grasslands from lowlands up to nearly 600 m a.s.l. in the Carpathian Basin (Thiele, 1977; Hůrka, 1996; Bérces *et al*., 2008). Adults are active from early spring to late fall with a lower peak of activity in May and June, and the main peak, representing the breeding period, from mid-August to September/October. Larvae hatch in late fall and pupate in the spring. Adults hatch from June to mid-July. Most adults overwinter and undergo aestivation dormancy (Bérces *et al*., 2007; Pokluda *et al*., 2007).

Carabus hungaricus is listed in Annexes II and IV of the EU Habitats Directive and is protected and/or red-listed in most countries of occurrence (Borodin *et al*., 1984; Shcherbak, 1994; Farkač *et al*., 2005; Bérces *et al*., 2008). It is near extinction in the Czech Republic, Slovakia (D. Čatloš, pers. comm.), and Austria (Arndt & Trautner, 2004). In the SE Czech Republic, for example, it was widely distributed in the first half of the 20th century, whereas just two localities are occupied at present (D. Hauck, P. Pokluda & L. Cizek, unpubl. data). Hungary, where *C. hungaricus* has recently been documented from numerous sites, represents the stronghold of the species in Central Europe. Even there, though, its populations are fragmented and isolated (Bérces *et al*., 2008).

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.) in SE Czech Republic. This National Nature Reserve and Site of Community Importance (total area: 180.8 ha), with *C. hungaricus* as one of its target species, represents one of the largest remnants of subcontinental steppic grasslands in the region. It is partly overgrown with shrubs and trees due to abandonment and hands-off conservation approach. Active management, consisting of grazing and mowing, was partly reestablished after 1989. In between, occasional fires together with numerous European rabbits (*Oryctolagus cuniculus*) prevented successional overgrowth of the steppe. The steppe is surrounded by agricultural land (arable fields, vineyards, orchards) and deciduous forests (Fig. 1). The topography is rugged with the bedrock consisting of claystone and sandstone, partly covered by loess. Mean annual temperature is 9.2 °C and mean annual rainfall nearly 500 mm (Mackovčin *et al*., 2007).

Sampling

Beetles were sampled using a capture-and-release approach with beer-baited pitfall traps. The bait was used to increase trapping efficiency (Fernández-Fernández & Salgado-Costas, 2004). The trap consisted of three plastic cups and a plastic rain shelter. The first cup (0.5 l; 9 cm diameter; 14 cm deep) was permanently placed in the ground and a second identical cup was inserted into the first one and served as a bait reservoir (about 10 ml of beer). Beetles were caught into the third cup (0.3 l; 8 cm diameter; 11 cm deep) that was inserted into the bait con-

© 2011 The Authors

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

taining cup. The third cup was perforated on side, so the bait aroma could permeate.

A total of 186 traps were positioned across the steppe and in its vicinity, distributed at various distances. The minimum distance between neighbouring traps was 5 m (mean: 18.65 m; SD: 17.74). Sampling focused on grasslands, but covered a wide range of habitats and vegetation types, including (roughly classified): arable field (seven traps), fallow (10), shortgrass steppe (19), tallgrass steppe and forest steppe (123), shrubby vegetation on the steppe (16), forest edge (0–5 m from the edge into the forest, 4), and closed-canopy forest interior (> 5 m from the edge, 7) (Fig. 1). Trapping covered the whole period of *C. hungaricus* activity, March 26th to November 6th, 2006. Traps were inspected, and the bait was replaced 1–2 times a week, summing 45 inspections in total. Beetles were released 2 m from the respective trap.

Together with sex and trap position of each trapped *C. hungaricus* individual, captures of 15 beetle species that are potential competitors (i.e., large carabids), and/or typical steppe dwellers of conservation interest were recorded (see Table 1). Habitat and vegetation characteristics were collected or estimated by an experienced botanist.

Variables

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

Beetle variables. (i) number of captures of *C. hungaricus* – total number of captures of *C. hungaricus* in each trap over the whole study period, and (ii) relative number of females – ratio of female captures to all *C. hungaricus* captures in each trap; (iii–xvii) number of captures of the 15 other beetle species – total number of captures of a given beetle species in each trap over the whole study period.

Vegetation variables. Percentage covers of the following vegetation types and selected indicative or otherwise noteworthy plants were estimated on three spatial scales (0.5 m, 2.5 m, and 5 m, within circles of the respective radius with trap in the centre): (i) 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 grasses, (ix) non-tussock grasses, (x) litter, (xi) mown – grasslands targeted by conservation management (mainly mowing); (xii) closed forest; (xiii) solitary woody plants (trees and shrubs taller than 50 cm), (xiv) short shrubs (< 50 cm), (xv) arable land, (xvi) feather grasses (*Stipa* spp.) – a dominant steppic grass, (xvii) liquorice (*Glycyrrhiza glabra*) – an exotic invasive species, and (xviii) wood small-reed (*Calamagrostis epigejos*) – a native species invading grasslands. Variables vi–ix lack 5 m scale since their estimation is reliable on short distances only. Nominal variable habitat (xix) reflects location of traps (see above).

Abiotic variables. (i) temperature, (ii) humidity, (iii) soil reaction, (iv) soil nitrogen content, (v) light, (vi) salinity, and (vii) gradient of slope (in degrees). Values of variables i–vi were estimated using plant-species data from plots around each trap (circle, 1 m diameter). The dataset contained 201 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 & Sýkora, 2000). We used values given by Borhidi (1995) for the Hungarian flora, summar-

© 2011 The Authors

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 and November 2006.

Beetle species	*n*	CS*
Darkling beetle (Tenebrionidae)		
Blaps lethifera (Marsham, 1802)	105	
Ground-beetles (Carabidae)		
Broscus cephalotes (Linnaeus, 1758)	5	
Calosoma auropunctatum (Herbst, 1784)	5	VU
Calosoma inquisitor (Linnaeus, 1758)	8	
Carabus coriaceus (Linnaeus, 1758)	235	
Carabus hortensis (Linnaeus, 1758)	21	
Carabus hungaricus (Fabricius, 1792)	3896	VU
Carabus nemoralis (O. F. Müller, 1764)	62	
Carabus ullrichi (Germar, 1824)	1340	
Longhorn beetles (Cerambycidae)		
Dorcadion fulvum (Scopoli, 1763)	25	D
Dorcadion pedestre (Poda, 1761)	25	D
Oil beetles (Meloidae)		
Meloe decorus (Brandt et Erichson, 1832)	45	
Meloe proscarabaeus (Linnaeus, 1758)	61	EN
Meloe scabriusculus (Brandt et Erichson, 1832)	16	NT
Meloe uralensis (Pallas, 1777)	60	CR
Meloe violaceus (Marsham, 1802)	5	VU

*Status follows Farkač *et al.* (2005) (CR, critically endangered; EN, endangered; VU, vulnerable; NT, nearly threatened) or species considered to be declining (D, cf. Sláma, 1998).

ised by Horváth *et al.* (1995). The values are relative, ranging 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 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

In all analyses, traps represented samples characterised by captures of sampled beetle species, surrounding vegetation, and abiotic factors.

The effect of habitat on *C. hungaricus* captures ($\log_e$-transformed) was investigated using one-way ANOVA, followed by Tukey's HSD test for unequal N.

The effect of vegetation on *C. hungaricus* captures was investigated using Generalised Linear Models (GLM). To establish spatial scale of the vegetation variables with the highest effect on *C. hungaricus* captures, full models (quasipoisson distribution of residual variability, log link function, explanatory variables $\log_e$-transformed) were separately fitted for the vegetation variables on the three spatial scales (0.5 m, 2.5 m, 5 m). Only the vegetation variables (i–v), (x), and (xii–xviii), 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, all the vegetation variables estimated for that scale entered further analyses. Their independent (marginal) effects on *C. hungaricus* captures were assessed using *F*-test. The effects of the vegetation variables on *C. hungaricus* captures were illustrated using a constrained linear ordination method, the redundancy analysis (RDA). The vegetation variables affecting *C. hungaricus* captures according to the above regression analyses were then used as response variables whilst the number of *C. hungaricus* captures acted as an explanatory variable (i.e., the vegetation variables were used as species data, number of *C. hungaricus* captures as an environmental variable). Variable mown, used as supplementary variable, did not enter the analysis, but was depicted to illustrate vegetation targeted by management. All variables were $\log_e$-transformed. Scaling focused on inter-species correlations, species scores were divided by standard deviations and species data were centred. Samples were neither centred nor standardised.

Independent effects of the abiotic variables on *C. hungaricus* captures were investigated using *F*-test (GLM, quasipoisson distribution of residual variability, log link function). Traps from closed-canopy forest interior and edge were omitted in all these analyses since these habitats are inappropriate for *C. hungaricus* as detected by the foregoing analyses.

Differences in habitat use as to the abiotic factors between sexes of *C. hungaricus* were ascertained using *F*-test (GLM, quasibinomial distribution of residual variability, logit link function). Relative number of females weighted by total number of captures acted as a dependent variable with abiotic variables as explanatory variables in separate analyses. To test the hypotheses that female habitat preferences do not differ during and outside the breeding period, the analyses were rerun separately with data from the whole season of activity except for the breeding period (March 26th–August 8th, 2006) and from the breeding period itself (August 9th–November 6th, 2006).

Distribution of all sampled beetle species in relation to each other was investigated using an unconstrained linear ordination, the principal component analysis (PCA). Captures of each species were square-root transformed. Scaling focused on inter-species correlations, species scores were divided by standard deviations and species data were centred. Samples were neither centred nor standardised.

Since independent effects of a high number of variables were investigated in GLM, significance level adjustment using Bonferroni correction was used. *P*-values between 0.05 and the adjusted value were considered marginally significant. Analyses were carried out using R 2.7.2 (Maindonald & Braun, 2003), Canoco for Windows 4.5 (Lepš & Šmilauer, 2003), and Statistica 8.0 StatSoft, Inc., (Hill & Lewicki, 2006).

Results

In total, 3896 captures of *C. hungaricus* (1792 male and 2100 female captures, sex not assessed in four cases) and 2018 captures of the 15 other beetle species were recorded (see Table 1). The mean number of *C. hungaricus* captures per trap was 20.9

© 2011 The Authors

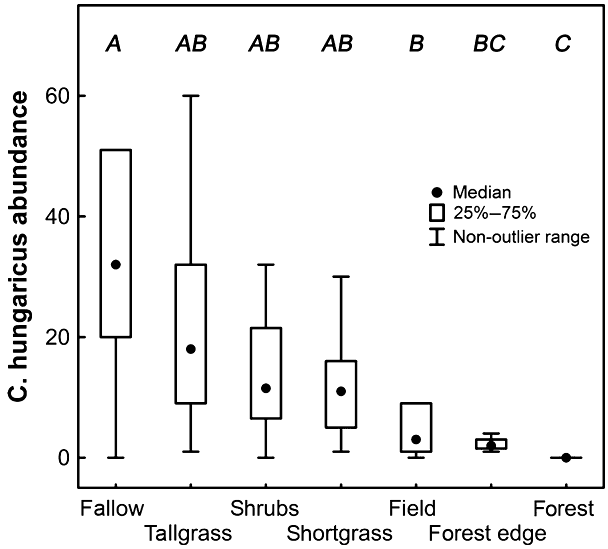

Fig. 2. Captures of *Carabus hungaricus* per trap in various habitats on the Pouzdrany steppe and its vicinity, Czech Republic, during 226 sampling days between March and November 2006. Letters indicate differences among habitats in number of *C. hungaricus* captures at pitfall traps placed in respective habitat ($P < 0.01$; Tukey Unequal N HSD test; data $\log_e$-transformed).

(SD: 22.8) from a total sampling effort of 42 036 trap-days (number of traps times number of sampling days). In a given habitat, mean number of *C. hungaricus* captures per trap and sampling effort (in trap-days) was as follows: arable fields (mean: 9.7; SD: 15.1; 1 582 trap-days), fallows (45.1; 43.7; 2 260), shortgrass steppe (11.6; 7.7; 4 294), tallgrass steppe and forest steppe (23.6; 22.1; 27 798), shrubby vegetation on the steppe (15.2; 12.1; 3 616), forest edge (2.3; 1.3; 904), and forest interior (0; 0; 1582). Habitat type had a strong effect on number of *C. hungaricus* captures ($F_{6,\ 179} = 16.93$; $P < 10^{-14}$; see Fig. 2 for details).

From the three spatial scales investigated, vegetation characteristics on the 2.5 m scale exhibited the strongest explanatory power on number of *C. hungaricus* captures (Model deviance MD = 1935.5; Mallows' Cp = 1921.5; d.f. = 13, 172; null model: Cp = 3576.5; d.f. = 185), while explanatory powers on 0.5 m (MD = 1831.4; Cp = 2025.5; d.f. = 13, 172) and 5 m scales (MD = 1794.5; Cp = 2062.5; d.f. = 13, 172) were weaker. At the 2.5 m scale, the number of *C. hungaricus* captures was positively affected by covers of herbs and grasses, tall grass, tall dicots, litter, and wood small-reed. Short dicots, closed forest, and feather grasses exhibited negative effects. The positive effects of total vegetation, broad-leaved herbs, and non-tussock grasses and the negative effect of solitary woody plants on number of *C. hungaricus* captures were marginally significant (Table 2; Fig. 3). Among the abiotic habitat characteristics, humidity and soil nitrogen affected number of *C. hungaricus* captures positively, while temperature, pH, light, and inclination had negative effects; salinity had no effect (Table 3). Humidity was strongly correlated with all other abiotic variables (separate rank correlations: temperature $r_s = -0.70$; $P < 10^{-6}$; pH $r_s = -0.71$; $P < 10^{-6}$; soil nitrogen $r_s = 0.86$; $P < 10^{-6}$; light $r_s = -0.58$; $P < 10^{-6}$; inclination $r_s = -0.35$; $P < 10^{-5}$), except for salinity ($r_s = -0.06$; $P = 0.4$).

Compared to males, *C. hungaricus* females preferred warmer, drier sites with more alkaline soil reaction and lower soil nitrogen content, and their proportion increased with inclination. The habitat selection between sexes differed only after start of

Table 2. Effect of vegetation on captures of *Carabus hungaricus* at pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. Independent effects of the percent cover of vegetation types in trap surroundings (within circle of 2.5 m radius) on number of *C. hungaricus* captures, as returned by *F*-test (Generalised Linear Models, quasipoisson distribution of residual variability, log link function, explanatory variables $\log_e$-transformed, $n = 186$).

Model	Regression coefficient *b*	d.f.	Residual deviance	Model deviance	*F*	*P*
Null		185	3555.0			
Total vegetation	0.79	1, 184	3387.0	168.0	7.13	*
Herbs and grasses	1.01	1, 184	2946.6	608.4	27.78	*****
Broad-leaved herbs	0.30	1, 184	3400.5	154.4	6.42	*
Short grass	−0.03	1, 184	3549.5	5.5	0.22	NS
Tall grass	0.53	1, 184	3023.7	531.3	23.92	*****
Short dicots	−0.31	1, 184	3281.7	273.3	12.35	***
Tall dicots	0.28	1, 184	3282.8	272.1	12.38	***
Tussock grasses	−0.09	1, 184	3511.6	43.4	1.78	NS
Non-tussock grasses	0.16	1, 184	3416.5	138.5	5.42	*
Litter	1.78	1, 184	3043.4	511.6	25.13	*****
Closed forest	−0.78	1, 184	3157.9	397.0	17.72	****
Solitary woody plants	−0.18	1, 184	3412.4	142.6	5.97	*
Short shrubs	0.08	1, 184	3515.5	39.5	1.56	NS
Arable land	−0.20	1, 184	3478.6	76.3	3.12	NS
Stipa spp.	−0.22	1, 184	3277.2	277.8	13.74	***
Glycyrrhiza glabra	−0.35	1, 184	3470.9	84.1	3.51	NS
Calamagrostis epigejos	0.24	1, 184	3155.5	399.5	19.01	****

P values after Bonferroni correction for 24 vegetation and abiotic variables: NS: $P > 0.05$; $0.05 > {*}P > 0.0021$; $0.0021 > {**}P > 0.001$; ${***}P < 0.001$; ${****}P < 0.0001$; ${*****}P < 0.00001$.

© 2011 The Authors

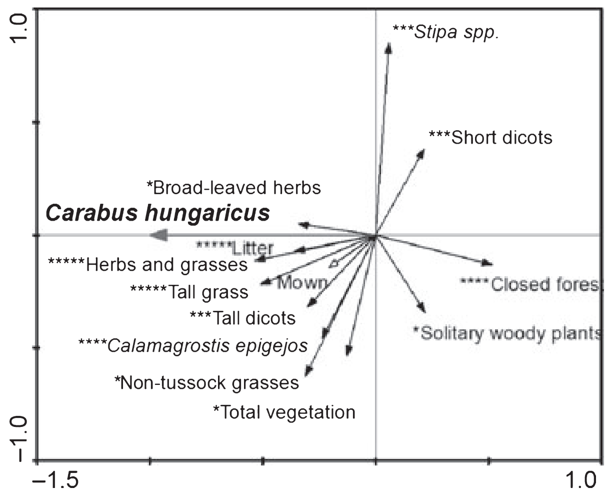

Fig. 3. Effect of vegetation on captures of *Carabus hungaricus* at pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. Illustrated using constrained ordination (redundancy analysis, 1st and 2nd ordination axes) and vegetation characteristics of trap surroundings within a circle of 2.5 m radius. Depicted variables affected *C. hungaricus* captures as returned by *F*-test, Generalised Linear Models (see Table 2). For the purpose of this illustration, the number of *C. hungaricus* captures at traps (grey arrow) acted as an explanatory variable, vegetation (black arrows) as response variables, and variable mown (blank arrow) as a supplementary variable. Canonical ordination axis accounted for 10.3% of the total variability (eigenvalue = 0.103; $F = 21.19$; $P < 0.001$). $0.05 > {}^{*}P > 0.0021$; $0.0021 > {}^{**}P > 0.001$; ${}^{***}P < 0.001$; ${}^{****}P < 0.0001$; ${}^{*****}P < 0.00001$.

the breeding period, but not during the rest of the season (Table 4).

PCA separated woodland beetles from dwellers of non-wooded habitats and *C. hungaricus* from all other grassland species (Fig. 4). The first (horizontal) axis separated species of non-wooded habitats from woodland dwellers, i.e., caterpillar hunter *Calosoma inquisitor* and ground-beetles of genus *Carabus* (except for *C. hungaricus*). The second (vertical) axis separated *Carabus hungaricus* from other grassland dwellers, i.e., longhorn beetles (*Dorcadion* spp.), caterpillar hunter *Calosoma auropunctatum*, oil beetles (*Meloe* spp.), and churchyard beetle *Blaps lethifera*. The first axis thus describes a gradient from grasslands to woodland, whereas the second axis represents a gradient of moisture or herb cover.

Discussion

Habitat preferences of Carabus hungaricus

Although a steppic grassland specialist, *C. hungaricus* prefers taller-vegetation patches with litter. It is most common in relatively humid parts of the steppe as well as in patches of taller vegetation at steppe margins, including fallows, field edges, and slopes of vineyard terraces. Thus, contrary to many species preferring short grass or even bare soil, it requires temporarily ungrazed/unmown, abandoned conditions. Both short-turf/-bare-soil patches and any woody structures, including solitary trees and shrubs, are avoided. Habitats of *C. hungaricus* thus should be managed to promote more advanced successional stages, with tall vegetation and accumulation of litter, but without woody vegetation.

Carabus hungaricus strictly avoids closed forests. Even narrow strips of closed woody vegetation likely form effective migration barriers. Invasion of woody plants into grasslands thus increases the extinction risk of *C. hungaricus* not only via direct habitat loss, but also due to population fragmentation. This is a serious concern in many *C. hungaricus* localities, where woody plants expand following management cessation. Records of *C. hungaricus* that appear to be from forests (Romania: Lie, 1995; Serbia: Pavićević & Mesaroš, 1997) contradict our findings and probably represent sampling artefacts (S. Bérces, pers. comm.).

The vegetation and abiotic variables revealed an identical pattern of preference for relatively humid conditions within steppes. The abiotic characteristics within the site are interconnected and affected by topography and vegetation. Thicker vegetation and litter (occurring mostly on flat sites and in depressions) slows evaporation, lowers solar radiation, and contributes to higher nutrient content. Such sites then host fewer xerophilous plants, which in turn promote lower temperature. The soil reaction is a marginal factor for ground-beetles (Thiele, 1977), and *C. hungaricus* inhabits localities with both acidic and basic reaction (Bérces *et al*., 2008). We therefore infer that moisture is the key factor

Table 3. Effect of abiotic characteristics on captures of *Carabus hungaricus* 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 *C. hungaricus* captures, as returned by *F*-test (Generalised Linear Models, quasipoisson distribution of residual variability, log link function). Traps from closed-canopy forest interior and edge were omitted ($n = 175$).

Model	Regression coefficient *b*	d.f.	Residual deviance	Model deviance	*F*	*P*
Null		174	3137.2			
Temperature	−1.37	1, 173	2447.7	689.4	46.10	*****
Humidity	0.61	1, 173	2801.6	335.6	18.08	****
Soil reaction	−0.73	1, 173	2853.5	283.6	14.55	***
Soil nitrogen content	0.26	1, 173	2939.5	197.7	9.81	**
Light	−0.87	1, 173	2891.3	245.8	12.65	***
Salinity	0.06	1, 173	3136.9	0.3	0.01	NS
Degree of slope	−0.03	1, 173	2913.5	223.7	11.03	**

P values after Bonferroni correction for 24 vegetation and abiotic variables: NS: $P > 0.05$; $0.05 > {}^{*}P > 0.0021$; $0.0021 > {}^{**}P > 0.001$; ${}^{***}P < 0.001$; ${}^{****}P < 0.0001$; ${}^{*****}P < 0.00001$.

© 2011 The Authors

Table 4. Sex-based differences in habitat use of *Carabus hungaricus* on the Pouzdrany steppe and its vicinity, Czech Republic. Independent effects of abiotic characteristics of trap surroundings (circle of 1 m diameter) on *C. hungaricus* female captures as a proportion of all *C. hungaricus* captures, as returned by *F*-test (Generalised Linear Models, quasibinomial distribution of residual variability, logit link function, $n = 176$). Three datasets of captures were used in separate analyses: (i) whole sampling period, (ii) before the start of breeding period, and (iii) from the start of breeding period onwards.

Model	Regression coefficient b	d.f.	Residual deviance	Model deviance	F	P
Whole sampling period						
Null		175	295.0			
Temperature	0.34	1, 174	283.3	11.7	7.81	**
Humidity	−0.32	1, 174	271.5	23.5	16.41	****
Soil reaction	0.37	1, 174	277.0	17.9	12.30	***
Soil nitrogen content	−0.18	1, 174	271.3	23.7	16.60	****
Light	0.21	1, 174	292.0	3.0	1.95	NS
Salinity	0.21	1, 174	294.3	0.7	0.46	NS
Degree of slope	0.02	1, 174	276.7	18.2	12.53	***
Before breeding						
Null		131	159.9			
Temperature	0.26	1, 130	158.7	1.2	1.17	NS
Humidity	−0.12	1, 130	159.4	0.5	0.53	NS
Soil reaction	0.21	1, 130	159.1	0.8	0.81	NS
Soil nitrogen content	−0.14	1, 130	158.3	1.6	1.61	NS
Light	0.14	1, 130	159.6	0.3	0.26	NS
Salinity	−0.14	1, 130	159.8	0.1	0.06	NS
Degree of slope	0.01	1, 130	158.5	1.4	1.40	NS
Breeding period						
Null		173	304.9			
Temperature	0.36	1, 172	293.8	11.1	7.17	*
Humidity	−0.34	1, 172	283.4	21.5	14.43	***
Soil reaction	0.38	1, 172	289.4	15.5	10.16	**
Soil nitrogen content	−0.17	1, 172	287.1	17.8	11.80	***
Light	0.25	1, 172	301.6	3.3	2.09	NS
Salinity	0.27	1, 172	304.0	0.9	0.58	NS
Degree of slope	0.02	1, 172	283.7	21.2	14.20	***

P values after Bonferroni correction for seven abiotic variables: NS: $P > 0.05$; $0.05 > {}^{*}P > 0.0071$; $0.0071 > {}^{**}P > 0.001$; $^{***}P < 0.001$; $^{****}P < 0.0001$.

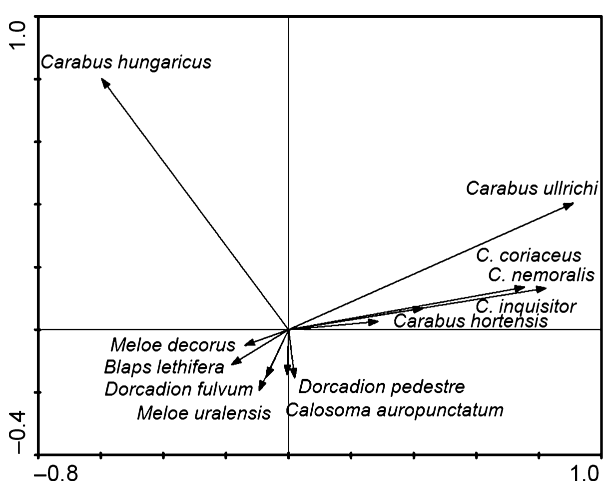

Fig. 4. Principal component analysis ordination comparing habitat preferences of beetles sampled by pitfall traps on the Pouzdrany steppe and its vicinity, Czech Republic. The first axis accounted for 54% and first two axes for 84% of the total variability (eigenvalues of first to fourth axes: 0.540; 0.299; 0.036; 0.027). Beetles with minimum fit = 2 are depicted. A clear separation of grassland and woodland species (horizontal axis), and *Carabus hungaricus* from all other grassland species (vertical axis) is apparent.

affecting local *C. hungaricus* distribution. Soil nutrient content indicating dense vegetation is also notable.

Habitat requirements of *C. hungaricus* differ from those of co-occurring large carabids. Ground-beetles of genus *Carabus* and the caterpillar hunter *Calosoma inquisitor* are associated mainly with woody vegetation, *Broscus cephalotes* with bare soil, and *Calosoma auropunctatum* with field/steppe (Hůrka, 1996). *Carabus hungaricus* apparently reaches high abundances at the study site, and likely lacks any closely related food competitors.

The preferences of *C. hungaricus* adults for overgrown steppic vegetation seemingly do not correspond with its overall distribution pattern. While its preferred habitats are relatively common, this originally rather widespread species is now surviving only on some of the largest, best preserved, and most heterogenous remnants of Pannonian steppes in the region. The area of habitat is likely to be an important factor for long-term survival of this large, flightless beetle (but see Matern *et al.*, 2008). Habitat requirements may also be affected by factors not covered by our study, such as larval habitat selection or diet (see below).

As *C. hungaricus* prefers taller-grass patches, the pattern of its distribution under traditional farming warrants explanation. Sites such as Pouzdrany steppe were originally used as grazing commons and thus were unlikely to offer suitable conditions. Instead, such conditions were likely found at field margins, fal-

© 2011 The Authors

lows and even mesic steppes, which used to alternate with arable lands even in the intensively farmed lowland region. As this network succumbed to intensification, species of marginal farmland biotopes retreated to formerly grazed and gradually overgrowing protected grasslands (cf. Fartmann, 2006).

Sex-based differences in habitat preferences

Females of *C. hungaricus* prefer warmer and drier sites than males during the breeding period. The sex-dependent differences in habitat use of ground-beetles are usually attributed to oviposition-site selection, as female habitat preferences change after copulation in some species (Thiele, 1977; Huk & Kühne, 1999). Limited mobility of preimaginal stages forces females to oviposit in habitat suitable for their offspring (Lövei & Sunderland, 1996). This explanation likely holds true also for *C. hungaricus*. Its larvae are active in cold and wet period of the year (Bérces *et al*., 2007; Pokluda *et al*., 2007) when temperature, rather than humidity, is the limiting factor. They thus may prefer drier/warmer parts of the steppe than summer-active, humidity-limited adults. The observed pattern can also be related to the larval need to escape predation by adults, or to unequal distribution of food supply (e.g., Kagawa & Maeto, 2009). The differences in habitat selection by adult sexes, and probably also by preimaginal stages, may broaden the range of habitats needed for survival of local populations (cf. Kagawa & Maeto, 2009), and this warrants further investigation.

Contrasting needs of grassland dwellers

A majority of the sampled grassland/steppe beetle species are threatened or declining (Table 1), but their habitat use differs from that of *C. hungaricus*. Although not yet studied in detail, our results indicate that these species avoid overgrown tall-grass steppe, preferring other vegetation phases instead: patches with short-turf, as in the cases of *Dorcadion fulvum* and *D. pedestre*, or patches of bare soil on paths, near burrows, on molehills, among tussocks, and within shortgrass vegetation, as in the cases of *Blaps lethifera*, *Meloe decorus* or *M. uralensis*.

These contrasting requirements highlight the necessity of spatially and temporarily diversified site management, which would support both species of short-turf and tall-grass. It has been repeatedly demonstrated that insects inhabiting apparently uniform habitat, such as dry grasslands, may differ in finer-level habitat requirements, which makes managing isolated insular remnants of rare habitats particularly challenging (Balmer & Erhardt, 2000; Bourn & Thomas, 2002; WallisDeVries *et al*., 2002).

Management recommendations

Overgrown, tall-grass with thick litter, and eutrophic steppe habitats are generally considered of lower conservation value than appropriately managed short-sward steppes (e.g., Stefanescu *et al*., 2009). Conservationists hence either strive to restore shorter-sward conditions or leave such sites to succession when resources for management are insufficient. The case of *C. hungaricus* demonstrates that even such habitats host their share of highly endangered grassland biodiversity.

On the other hand, *C. hungaricus* is not the only species whose needs have to be accommodated by the site management. Most lowland grasslands in intensively farmed Central Europe exist as islands within inhospitable landscapes, thus hosting isolated invertebrate populations, which cannot be replenished in case of local extinction (Wenzel *et al*., 2006). As with all species-rich grassland reserves (Morris, 2000), sites with *C. hungaricus* must be managed to support diverse arrays of species with differing requirements for vegetation height, humidity, presence or absence of bare soil, and other factors. To preserve the diverse conditions, sites must be managed in a patchy manner, with alternating areas in various successional stages (Balmer & Erhardt, 2000; Kruess & Tscharntke, 2002; WallisDeVries *et al*., 2002; Pöyry *et al*., 2004). For the study site, we recommend temporarily varying rotational grazing accompanied by mowing. Sizeable proportions of the locality should be left unmanaged for 5–10 years, to allow for regeneration of tall-grass conditions with accumulation of litter, but to prevent succession towards scrub. Invasive woody species should be removed without exception, with indigenous species removed selectively, leaving solitary individuals or small groups untouched.

The ability of *C. hungaricus* to occupy fallows, and to cross hundreds of metres of unfavoured non-forest habitats (e.g., arable land; P. Pokluda, D. Hauck & L. Cizek, unpubl. data), offer a chance to return the species to the wider environs of current localities within an intensively used agricultural landscape. Such a return requires restoring a system of small steppe enclaves, grassland strips, and fallow patches. It would sustain long-term survival of *C. hungaricus*, increase biodiversity in arable systems and support species of economic value, e.g., pollinators and game (Balmer & Erhardt, 2000; Thomas *et al*., 2001; Bäckman & Tiainen, 2002; Noordijk *et al*., 2009).

Acknowledgements

We thank K. Chobot and J. Mourek for support; S. Bérces, J. Dovala, and V. Kubáň assisted with field work; P. Kepka, M. Konvička, and P. Šmilauer assisted with analyses; D. Čatloš, M. Danilevsky, A. Lozan, J. Miklín, F. Rosypal, P. Saska, and M. Sweney assisted with other aspects of the study; two anonymous reviewers and N. A. Littlewood helped to improve the article. The study was supported by the Czech Academy of Sciences (KJB600960705), the Czech Ministry of Education (6007665801 and LC06073), and the Agency for Nature Conservation and Landscape Protection of the Czech Republic.

References

Alonso, J.C., Martín, C.A., Alonso, J.A., Palacín, C., Magana, M., Lieckfeldt, D. & Pitra, C. (2009) Genetic diversity of the great bustard in Iberia and Morocco: risks from current population fragmentation. *Conservation Genetics*, **10**, 379–390.

© 2011 The Authors

Arndt, E. & Trautner, J. (2004) Carabini. *Band 2. Adephaga 1: Carabidae (Laufkäfer)* (ed. by G. Müller-Motzfeld). *Die Käfer Mitteleuropas* (ed. by H. Freude, K.W. Harde, G.A. Lohse and B. Klausnitzer), pp. 30–60. Spektrum-Verlag (Heidelberg – Berlin), 2. Auflage (in German).

Bäckman, J.-P.C. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture, Ecosystems and Environment*, **89**, 53–68.

Balmer, O. & Erhardt, A. (2000) Consequences of succession on extensively grazed grasslands for Central European butterfly communities: rethinking conservation practices. *Conservation Biology*, **14**, 746–757.

de Bello, F., Lavorel, S., Gerhold, P., Reier, Ü. & Pärtel, M. (2010) A biodiversity monitoring framework for practical conservation of grasslands and shrublands. *Biological Conservation*, **143**, 9–17.

Bérces, S., Soltész, Z., Szél, G. & Peregovits, L. (2007) Seasonal activity, and population size of *Carabus hungaricus* Fabricius, 1792 in a pannonic sand steppe habitat in Hungary (poster). *Back to the roots or back to the future? Towards a New Synthesis Between Taxonomic, Ecological and Biogeographical Approaches in Carabidology* (ed. by L. Penev), pp. 81. XIII European Carabidologists Meeting, Blagoevgrad, August 20–24 Abstract Volume and Programme. Pensoft Publishers, Sofia and Moscow.

Bérces, S., Szél, G., Ködöböcz, V. & Kutasi, C. (2008) The distribution, habitat, and the nature conservation value of a Natura 2000 beetle, *Carabus hungaricus* Fabricius, 1792 in Hungary. *Back to the Roots and Back to the Future. Towards a New Synthesis Between Taxonomic, Ecological and Biogeographical Approaches in Carabidology* (ed. by L. Penev, T. Erwin and T. Assmann), pp. 363–372. Proceedings of the XIII European Carabidologists Meeting, Blagoevgrad, August 20–24, Pensoft Series Faunistica No. 75. Pensoft Publishers, Sofia and Moscow.

Binot, M., Bless, R., Boye, P., Gruttke, H. & Pretscher, P. (1998) *Rote Liste gefährdeter Tiere Deutschlands. Schriftenreihe für Landschaftspflege und Naturschutz 55*. Bonn-Bad Godesberg, Germany (in German).

Borhidi, A. (1995) Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica*, **39**, 97–181.

Borodin, A.M., Bannikov, A.G. & Sokolov, V.E. (ed.) (1984) *Red Book of USSR. Rare and Endangered Species of Animals and Plants*, 2nd edn. Lesnaya Promyshlennost' Publishers, Moscow, Russia (in Russian).

Bourn, N.A.D. & Thomas, J.A. (2002) The challenge of conserving grassland insects at the margins of their range in Europe. *Biological Conservation*, **104**, 285–292.

Bousquet, Y., Březina, B., Davies, A., Farkač, J. & Smetana, A. (2003) Tribe Carabini Latreille, 1802. *Catalogue of Palearctic Coleoptera. Vol. 1. Archostemata – Myxophaga – Adephaga* (ed. by I. Löbl and A. Smetana), pp. 118–201. Apollo Books, Stenstrup, Denmark.

Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A. & Baur, B. (2005) Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conservation Biology*, **19**, 1606–1618.

Dúbravková, D., Chytrý, M., Willner, W., Eszter, I., Janišová, M. & Kállayné Szerényi, J. (2010) Dry grasslands in the Western Carpathians and the northern Pannonian Basin: a numerical classification. *Preslia*, **82**, 165–221.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa, 2nd edition. *Scripta Geobotanica*, **18**, 1–258 (in German, English summary).

Farkač, J., Král, D. & Škorpík, M. (eds) (2005) *Červený seznam ohrožených druhů České republiky. Bezobratlí. Red List of Threatened Species in the Czech Republic. Invertebrates*. AOPK ČR, Prague, Czech Republic (in Czech).

Fartmann, T. (2006) Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. *Annales Zoologici Fennici*, **43**, 335–347.

Fernández-Fernández, M.M. & Salgado-Costas, J.M. (2004) Recolonization of a burnt pine forest (*Pinus pinaster*) by Carabidae (Coleoptera). *European Journal of Soil Biology*, **40**, 47–53.

Gepp, J. (ed.) (1994) *Rote Listen gefährdeter Tiere Österreichs*. Bundesministerium für Umwelt, Jungend und Familie, Graz, Austria (in German).

Guéorguiev, V.B. & Guéorguiev, B.V. (1995) *Catalogue of the Ground-Beetles of Bulgaria (Coleoptera: Carabidae)*. Pensoft Series Faunistica No. 2. Pensoft Publishers, Sofia and Moscow.

Hill, T. & Lewicki, P. (2006) *Statistics: Methods and Applications. A Comprehensive Reference for Science, Industry, and Data Mining*. StatSoft, Inc., Tulsa, Oklahoma.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.

Horváth, F., Dobolyi, Z.K., Morschhauser, T., Lökös, L., Karas, L. & Szerdahelyi, T. (1995) *FLÓRA adatbázis 1.2 – Taxonlista és attribútum-állomány*. Hungarian Academy of Sciences, Vácrátót, Hungary (in Hungarian).

Huk, T. & Kühne, B. (1999) Substrate selection by *Carabus clatratus* (Coleoptera, Carabidae) and its consequences for offspring development. *Oecologia*, **121**, 348–354.

Hulová, Š. & Sedláček, F. (2008) Population genetic structure of the European ground squirrel in the Czech Republic. *Conservation Genetics*, **9**, 615–625.

Hůrka, K. (1996) *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlín, The Czech Republic.

Käfer, J. & Witte, J.-P.M. (2004) Cover-weighted averaging of indicator values in vegetation analyses. *Journal of Vegetation Science*, **15**, 647–652.

Kagawa, Y. & Maeto, K. (2009) Spatial population structure of the predatory ground beetle *Carabus yaconinus* (Coleoptera: Carabidae) in the mixed farmland-woodland satoyama landscape of Japan. *European Journal of Entomology*, **106**, 385–391.

Konvička, M., Beneš, J., Čížek, O., Kopeček, F., Konvička, O. & Vitaz, L. (2008) How too much care kill species: grassland reserves, agri-environmental schemes and extinction of *Colias myrmidone* (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect Conservation*, **12**, 519–525.

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, **16**, 1570–1580.

Leather, S.R., Basset, Y. & Hawkins, B.A. (2008) Insect conservation: finding the way forward. *Insect Conservation and Diversity*, **1**, 67–69.

Lepš, J. & Šmilauer, P. (2003) *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge, UK.

© 2011 The Authors

Lie, P. (1995) Beiträge zur Kenntniss des *Carabus hungaricus frivaldskyanus* Breuning neuentdeckt im Banat, Rumänien (Coleoptera, Carabidae). *Folia Entomologica Hungarica*, **56**, 85–88 (in German).

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231–256.

Mackovčin, P., Jatiová, M., Demek, J. & Slavík, P. (eds) (2007) Brněnsko. *Chráněná území ČR, svazek IX* (ed. by P. Mackovčin), pp. 1–932. AOPK ČR a EkoCentrum, Praha (in Czech).

Maindonald, J.H. & Braun, W.J. (2003) *Data Analysis and Graphics Using R. An Example-Based Approach*. Cambridge University Press, Cambridge, UK.

Marini, L., Fontana, P., Battisti, A. & Gaston, K.J. (2009) Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. *Insect Conservation and Diversity*, **2**, 213–220.

Matern, A., Drees, C., Meyer, H. & Assmann, T. (2008) Population ecology of the rare carabid beetle *Carabus variolosus* (Coleoptera: Carabidae) in north-west Germany. *Journal of Insect Conservation*, **12**, 591–601.

Morris, M.G. (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, **95**, 129–142.

Noordijk, J., Delille, K., Schaffers, A.P. & Sýkora, K.V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, **142**, 2097–2103.

Pavićević, D. & Mesaroš, G. (1997) *Carabini of Jugoslavia and adjacent regions (Coleoptera: Carabidae). Catalogus Faunae Jugoslaviae. Encyclopaedia*. Ecolibri-Bionet, Belgrade, Serbia and Montenegro. Released on CD-ROM.

Pokluda, P., Hauck, D. & Čížek, L. (2007) Habitat preferences, population structure and mobility of the ground beetle *Carabus hungaricus* in the Pouzdrany steppe. *Fauna Pannonica 2007, Symposium on Conservation and Genesis of the Fauna of the Carpathian Basin, Kecskemét, Hungary, November 29 – December 1, 2007. Abstracts* (ed. by P. Batáry and Á. Körösi), pp. 55. Hungarian Natural History Museum, Budapest.

Pöyry, J., Lindgren, S., Salminen, J. & Kuussaari, M. (2004) Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications*, **14**, 1656–1670.

Schaffers, A.P. & Sýkora, K.V. (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science*, **11**, 225–244.

Shcherbak, M.M. (ed.) (1994) *Chervona knyha Ukrainy. Tvarynnyi svit. Red Data Book of Ukraine. Animal Kingdom.* Ukrainska Encyclopedia, Kiev, Ukraine (in Ukrainian).

Skaloš, J. (2006) Collectivisation of agriculture reflected in the farming landscape of the eastern Czech Republic between 1937 and 2002, aerial photography analysis. *Abstract Volume of the 4th International Interdisciplinary Conference on Rural Landscape, Slavičín and Hostětín, May, 12–14, 2006* (ed. by Anonymous), pp. 177–182. ZO ČSOP Veronica, Brno.

Sláma, M.E.F. (1998) *Long-Horned Beetles (Cerambycidae) of the Czech Republic and the Slovak Republic (Beetles – Coleoptera)*. Milan Sláma, Krhanice (in Czech).

Stefanescu, C., Peñuelas, J. & Filella, I. (2009) Rapid changes in butterfly communities following the abandonment of grasslands: a case study. *Insect Conservation and Diversity*, **2**, 261–269.

Thiele, H.U. (1977) *Carabid Beetles in their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer, Berlin.

Thomas, S.R., Goulson, D. & Holland, J.M. (2001) Resource provision for farmland gamebirds: the value of beetle banks. *Annals of Applied Biology*, **139**, 111–118.

Turin, H., Penev, L. & Casale, A. (eds) (2003) *The Genus Carabus in Europe. A Synthesis. Fauna Europea Evertebrata. No 2.* Co-published by Pensoft Publishers, Sofia – Moscow and European Invertebrate Survey, Leiden.

Veselý, P. (2002) *The Mohelno serpentine steppe – On the origin and history of the reserve and its research*. Mendel University of Agriculture and Forestry, Brno (in Czech).

WallisDeVries, M.F., Poschlod, P. & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, **104**, 265–273.

Wenzel, M., Schmitt, T., Weitzel, M. & Seitz, A. (2006) The severe decline of butterflies on western German calcareous grasslands during the last 30 years: a conservation problem. *Biological Conservation*, **128**, 542–552.

Woodcock, B.A., Edwards, A.R., Lawson, C.S., Westbury, D.B., Brook, A.J., Harris, S.J., Brown, V.K. & Mortimer, S.R. (2008) Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. *Oecologia*, **154**, 773–783.

Accepted 9 March 2011
First published online 11 October 2011

Editor: Alan Stewart
Associate editor: Nick Littlewood

© 2011 The Authors