

University of South Bohemia in České Budějovice

Faculty of Science

Department of Zoology

**How life history affects threat status: Requirements of two
Onobrychis-feeding lycaenid butterflies, *Polyommatus damon* and
Polyommatus thersites, in the Czech Republic**



RNDr. Thesis

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Anotation

The study compares ecological requirements of two related (congeneric) butterflies, *Polyommatus damon* and *P. thersites*, both of them reaching their northern distribution margins in Central Europe, where they co-occur on xeric grasslands, utilising identical larval host plants. Despite these similarities, one of them is substantially more endangered than the other. We describe their egg-laying behaviour and egg placement patterns, and analyse their distribution in a model landscape, showing that minute life history details affect differing species' fates in human-dominated landscapes.

Declaration (in Czech)

Prohlašuji, že svoji rigorózní práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Co-authors agreement

The co-authors listed below fully acknowledge that Jana Šlancarová significantly contributed to this publication. Jana was the first and corresponding author of this study and was involved in all stage of the study. She was responsible for field sampling, analysed the data and contributed also to manuscript writing. The article is based on her bachelor thesis.

The co-authors hereby consent to the publication in the RNDr. thesis of Jana Šlancarová and support this statement with their signatures (without academic titles):

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How life history affects threat status: Requirements of two *Onobrychis*-feeding lycaenid butterflies, *Polyommatus damon* and *Polyommatus thersites*, in the Czech Republic

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Abstract: Comparisons of related species differing in conservation status may offer insights into causes of species declines. We studied egg-laying patterns and landscape occupancy of two sympatric lycaenidae butterflies inhabiting xeric grasslands, vulnerable *Polyommatus thersites* and critically endangered *Polyommatus [Agrodiaetus] damon*, both developing on sainfoin, *Onobrychis* spp. Females of bivoltine *P. thersites* oviposit on host plant leaves at a relatively low height (≈ 20 cm), in both spring (May–June) and summer (July–August) generations. Females of univoltine *P. damon* (July–September) oviposit on senescing inflorescences, in significantly higher heights (>30 cm), and the species is hence vulnerable to summer mowing or grazing. On a landscape scale, both species tended to occur at sites with diverse sward management, including temporarily unmanaged patches. In addition, *P. damon* occurred only in the proximity of other occupied sites. The study documents that grassland management must respect the needs of the most vulnerable species, and because these needs are seldom known, it must maintain a high diversity of conditions within individual sites.

Key words: butterfly conservation; farmland landscape; grazing; habitat management; insect life history; Lepidoptera; metapopulation; xeric grassland

Introduction

Profound land use changes such as agriculture and forestry intensification, urbanisation and abandonment of marginal lands, has resulted into biodiversity loss across Europe during the last decades (Donald et al. 2001; Kleijn et al. 2009; Stoate et al. 2001). In the model group of butterflies, one third of European species is declining (Van Swaay et al. 2010) and even worse situation applies in individual countries, such as the Czech Republic, where declines have affected about half the fauna (Beneš et al. 2002; Konvička et al. 2006). Species of seminatural grasslands rank among the most severely affected ones, because these biotopes have been maintained for centuries by traditional, and now obsolete, land use techniques (Brereton et al. 2008; Poschlod et al. 2005). Xeric grasslands of Northern and Central Europe, where many species find their northern distribution margins, seem to be particularly suffering due to the concentration of such grasslands in warm regions suitable for intensive agriculture (Kadlec et al. 2010; Thomas 1993). Resulting declines of warm-dependent species near range margins represent a paradox, because if suitable habitats would be present, such species should be increasing under the currently warming climate (Warren et al. 2001). It is increasingly agreed

that fragmented remnants of xeric grasslands, often protected as reserves, are insufficient to support the regional diversity of xerophilous species (Kadlec et al. 2008; Sang et al. 2010; Wenzel et al. 2006).

Not all xeric grassland butterflies are affected at the same rate. The fate of particular species depends on a combination of species-specific habitat requirements, supply of potential habitats (area, connectivity) in a given region, and habitat quality, which can be manipulated by management of remnant habitat patches (Krauss et al. 2005; Rosin et al. 2011; Thomas et al. 2001). Because management actions appropriate for one species may directly harm others (Bourn & Thomas 2002; Dolek & Geyer 2002), diversified land management offers the only chance to secure diverse arrays of specialised species both within insular reserves and in surrounding landscapes (Čížek L. et al. 2012; Morris 2000; Oliver et al. 2010). A way to understand how life history, site quality and landscape factors interact in affecting individual species fates is studying pairs of co-occurring related species that differ in severity of their declines. Such studies have revealed such threat factors as insufficient immigration (Murphy et al. 1986), decreased host plant accessibility (Samways & Lu 2007) and inappropriate management (Turlure et al. 2010).

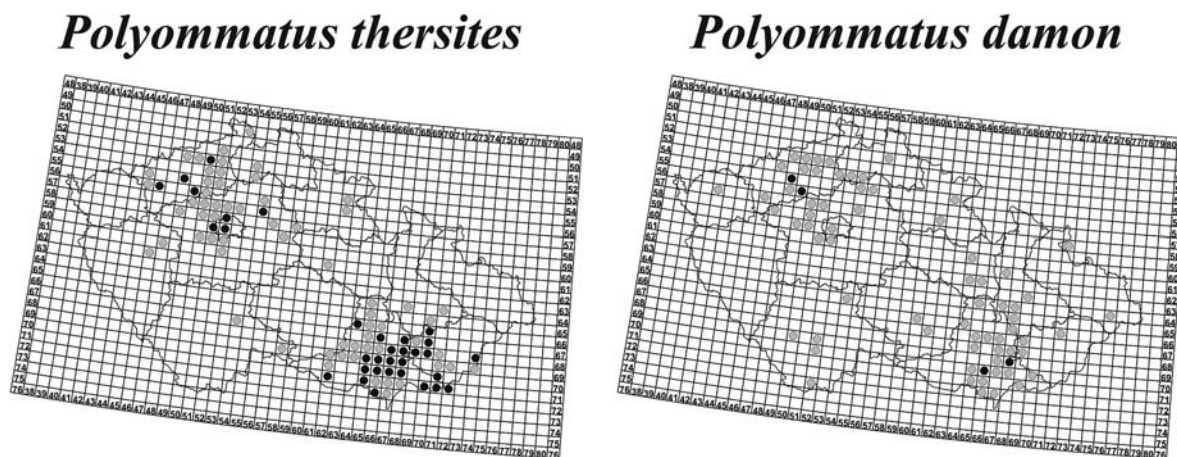


Fig. 1. Grid maps of the Czech Republic, showing historical and current (post-2005) records of *Polyommatus thersites* and *P. damon*. Although gradual decline is apparent in both species, it is much more severe in the latter. Data were obtained from the Czech butterfly and moth recording scheme and Beneš et al. (2002). Symbols: grey circles: pre-2001 records, black circles: 2002–2011 records.

Here, we ask how life history, within-habitat factors and landscape factors affect a pair of related lycaenid butterflies that use the identical host plant, the sainfoin (*Onobrychis* spp.) on xeric grasslands near their northern distribution margins in the Czech Republic. Both studied species have declined in the country, *Polyommatus thersites* (Cantener, 1835) by 62 per cent of its 1950s distribution, and *Polyommatus damon* (Denis & Schiffermüller, 1775) even more severely, by 94 per cent (Beneš et al. 2002; and unpublished data from Czech butterfly and moth recording scheme). The same situation applies across Central Europe (Ebert & Rennwald 1991; Nässig et al. 2004; Zsolt 2004). Several authors have attributed *P. damon* declines to its intolerance of grazing, especially by sheep, which is routinely used to maintain xeric grasslands in the region (Dolek 1994; Dolek & Geyer 2002; Kudrna 1998). The evidence remains anecdotal, however, as none of the two species have been studied in detail.

We carried out focal observations of ovipositing females, at a site where both species co-occur, asking which host plants parts, and phenological states, are utilised for oviposition, and hence larval development. Next, we compared the presence and abundance of both species in a wider landscape, constructing regression models that consider site quality, management, and among-sites connectivity. Finally, we combine the life history and occurrence patterns to sketch a conservation strategy for the two butterflies.

Material and methods

Study species

Both *Polyommatus thersites* and *P. damon* are restricted to xeric grasslands in Central Europe (Beneš et al. 2002; Weidemann 1995). They develop on sainfoins, represented by *Onobrychis arenaria* (Kitaibel) and *O. viciifolia* (Scopoli) in the Czech Republic.

Polyommatus thersites is bivoltine, overwintering as young larva and forming the first adult generation from late April until June and second adult generation from June until

September (Tolman & Lewington 2009). Larvae are facultatively myrmecophilous (Fiedler 2006; Mihoci & Šašić 2006). Its total distribution stretches from Morocco through Southern and Central Europe to Tian Shan in the East (Tolman & Lewington 2009); the northern distribution margin crosses Central Germany and southern Poland (Kudrna 2002). Unlike in Southern Europe, where it can occur at high elevations, the occurrence in Central Europe is restricted to warm lowland areas. In the Czech Republic, the distribution follows the warmest regions both in western (i.e., Bohemia) and eastern (i.e., Moravia) parts of the country (Fig. 1). It forms spatially restricted colonies closely associated with host plants occurrence, and is classified as endangered in the country (Farkač et al. 2005).

P. damon is univoltine, with adults occurring in late summer (mid-July – early September). The overwintering stage is an early-instar larva (Ebert & Rennwald 1991; Nässig et al. 2004; Weidemann 1995). Larvae are again facultatively myrmecophilous (Fiedler 2006; Mihoci et al. 2006). The distribution stretches from the Iberian Peninsula and all of Southern Europe to Mongolia in the east (Gorbunov 2001; Tolman & Lewington 2009). In Central Europe, it includes Switzerland, Southern Germany (rapidly decreasing), the Czech Republic, Slovakia (no recent data) and southern Poland (extinct: Buszko & Maslowski 2008). In the Czech Republic, it currently survives in two disjunct areas, Ceske Stredohori Highlands (Northwest), and southeastern Moravia (Fig. 1) and is classified as critically endangered (Beneš et al. 2002; Farkač et al. 2005).

Study area

The study was conducted in southeastern Moravia, a north-western promontory of the Pannonian biogeographic district (Fig. 2). It is a low-elevated region (maximum altitude: 383 m a.s.l.) covered by flat river plains separated by rolling hills, with continental warm (mean annual temperature: 8.3°C) and dry (annual rainfall 500–550 mm) climate. The region is renowned for fertile soils and intensive agriculture (about 80% of the area is farmland, including vineyards and intensive orchards). Woodlands are sparse, mainly represented by oak-hornbeam forests. Xeric grasslands, habitat of the studied species, are preserved in only tiny remnants, usually on steeper slopes on base-rich loess bedrock, which

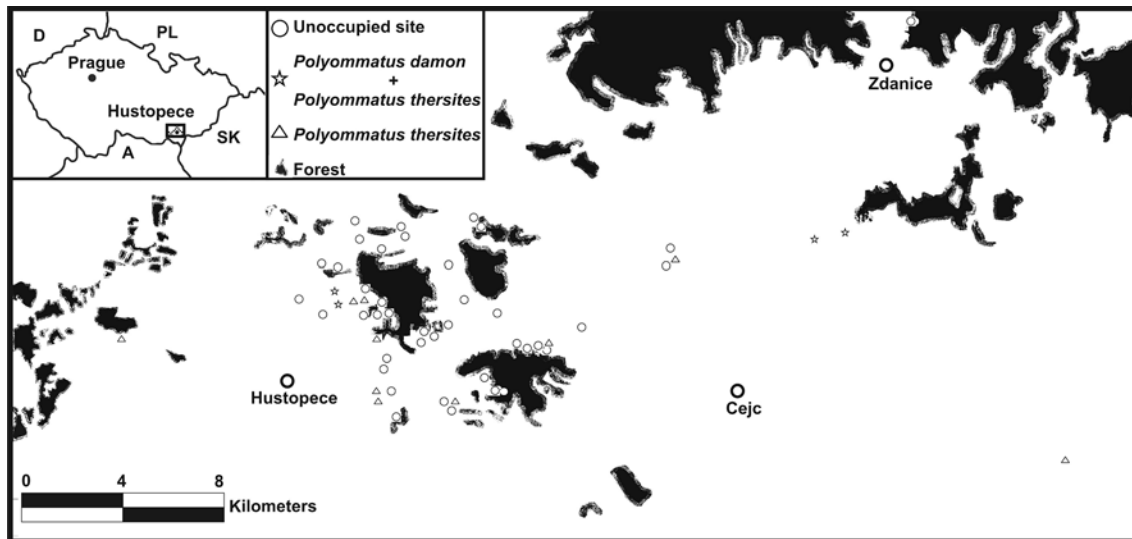


Fig. 2. A map of sites visited while studying landscape occupancy by *Polyommatus thersites* and *P. damon* in southeastern Moravia, Czech Republic.

were historically used for grazing, and now are mostly protected as nature reserves (cf. Pokluda et al. 2011).

Oviposition patterns

Detailed study of both species was carried out at Kamenný vrch (48°57'56" N, 16°45'12" E, altitude 343 m), a 65 ha reserve near Kurdějov village. Valued as one of the best-preserved islands of steppic grasslands in southeastern Moravia (Chytrý et al. 2001), it is situated at a west-oriented loess slope, at an altitude of 276–343 m a.s.l. Formerly a grazing commons, it is now covered by a mosaic of xeric grasslands and scrub in varying successional stages. It is surrounded mainly by farmland, vineyards and gardens.

During adult flight (*P. thersites* 1st generation: May – June 2008 and 2010; 2nd generation and *P. damon*: July – September 2008 and 2010), we observed females' activity using focal observation. The visits were limited to 11:30–16:30 (CEST) and to suitable weather (over 25°C, sunny, none to mild wind). Once a female was spotted, we followed it closely with a digital sound recorder, recording her activity.

Whenever oviposition was observed, we searched for eggs laid, and recorded the following characteristics of oviposition substrate: (i) Sainfoin density, in a 5 m diameter circle (ranked variable: 0 – None, 1 – Individual plants, 2 – Prominent clumps, 3 – Continuous cover). (ii) Sainfoin phenology, based on a majority of flowers present: Not flowering, Flowering, Fruiting. (iii) Egg location: Stem, Leaf, Bract, Flower, Grass. (iv) Egg location height. (v) Sainfoin height. (vi) Sward height, measured at a typical point within a one-metre diameter from the plant.

Landscape occupancy patterns

To ascertain the distribution patterns of both species, we surveyed a total of 54 xeric grassland sites in wider environs of the Kamenný vrch reserve. The selection of sites included all *P. damon* ($n = 4$) sites known in the region according to the Czech butterfly and moth recording scheme, plus a majority of prominent xeric grassland islets, both protected as reserves and not-protected, within an area of 200 km² (Fig. 2, Appendix 1).

All sites were visited during the period of joint flight of both species, some of them repeatedly to cover both

spring (hereafter *thersites1*) and summer (hereafter *thersites2*) *P. thersites* flight. During each visit, we thoroughly searched the site, focusing on sainfoin patches and trying to locate as many individuals of the targeted species. We recorded the butterflies using a semiquantitative abundance, using the scale: 1 – one individual, 2 < 10, 3 < 100, and 4 – hundreds of individuals.

The following site characteristics were recorded for each site: (i) Number of visits (hereafter Visits), as a nuisance variable in regression models. (ii) Geography variables: Longitude, Latitude and Altitude. (iii) Site conditions: Area, Slope (difference between the highest and lowest contour line); Orientation (expressed as a ranked variable: SW, S – 5; SE, W – 4; flat – 3; NW, E – 2; N, NE – 1); Sainfoin density (ranked scale; 0 – none, 1 – individual plants, 2 – prominent clumps, 3 – continuous cover). (iv) Habitat types within each site, expressed as proportional representation of Xeric grassland, Ruderal grassland, Abandoned orchard, Woodland edges, Terraces (built during intensification efforts in the past and now abandoned), Field banks, Clearings. (v) Management, expressed as a proportion of total site area subject to given management and distinguishing Mowing, Grazing, and Neglect. (vi) Relative site connectivity, expressed as the distance to the closest *P. thersites* site (herein closest *thersites*), the closest *P. damon* site (herein closest *damon*), and a mean distance to three closest xeric grasslands (herein three steppes). Distances were obtained from online application of the official real estate register (<http://nahlizenidokn.cuzk.cz/>).

We constructed regression models for presence and (semiquantitative) abundance of each of the species (i.e., four dependent variables) on the sites, using generalised linear models in S-plus 8.0 Software (TIBCO). For the sites that were visited repeatedly, we considered the visit with the highest observed abundance of modelled species, and, assuming that detection probability increases with effort, considered Visits as a covariable in the models. Presence data were modelled using logit link and binomial errors distribution; abundance data using log link and Poisson's error distribution. Model selection was based on information theory (Akaike 1974), using the Cp statistics incorporated to S-plus.

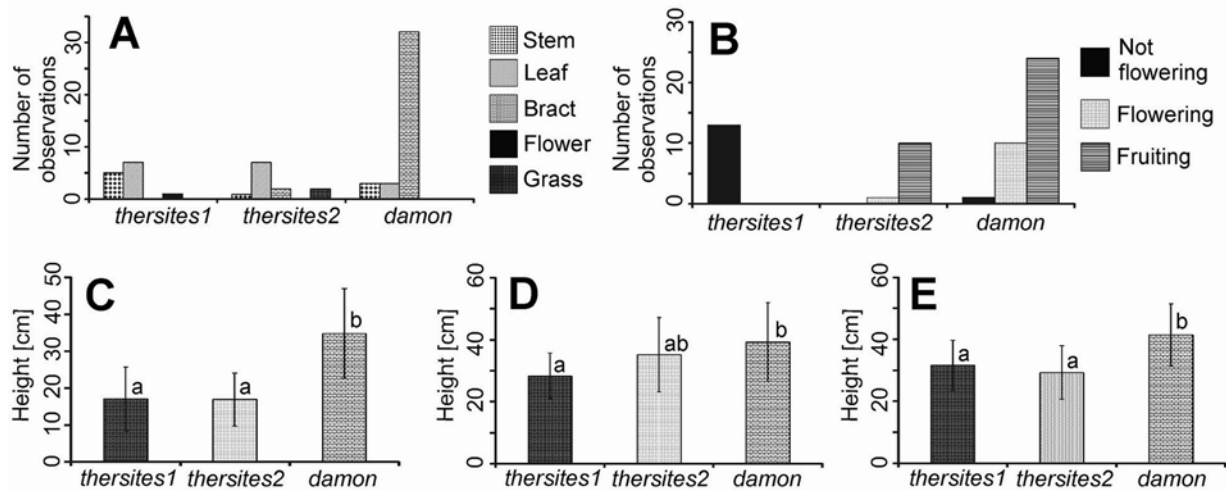


Fig. 3. Oviposition patterns of females of spring and summer generations of *Polyommatus thersites* (*thersites1*, *thersites2*) and *P. damon* (*damon*), recorded in sympatry in southeastern Moravia, Czech Republic. (A) Egg location on host plant (*Onobrychis* spp.), (B) Sainfoin phenology during the oviposition, (C) Egg location height, (D) Sainfoin height, (E) Surrounding Sward height. Graphs C–E show means \pm standard errors, the letters a, b show differences among means, as revealed by Kruskal-Wallis ANOVA.

We first ascertained the independent effects of single predictors, using single-term regressions. Next, we computed models based on Visits and geography variables, because these predictors influence species occurrence (Geography) or detection (Visits), and are herein considered as covariables. A stepwise forward selection of predictors was used to obtain *covariate models*. We then repeated the single-term tests on the covariate models. Finally, we constructed multiple regression models based on forward stepwise addition of terms to *covariate models*, to study the combination of factors influencing the studied species presence and abundance.

Results

Female oviposition patterns

We observed totals of 48, 47 and 155 oviposition events by 14, 22 and 47 females of *thersites1*, *thersites2* and *damon*, respectively. When settled, *P. thersites* females crawled on sainfoin stems down to leaf rosettes, whereas *P. damon* females searched within the inflorescence. The respective numbers of eggs actually found were 13, 12 and 38. In both species, eggs were laid either singly, but some females laid several eggs during a single egg-laying event: two ($n = 2$) and four ($n = 1$) eggs in *thersites1*, two ($n = 2$) in *thersites2*, and two ($n = 5$) or three ($n = 2$) in *damon*.

Comparing sainfoin density within 5 m diameter circles around the egg-laying spots did not show any difference between *thersites1*, *thersites2* and *damon* (Kruskal-Wallis test: $H(13, 57) = 8.48$, $P = 0.81$). Median ranked value for sainfoin density was 2 for all three groups compared, indicating that clumped sainfoins prevailed.

Regarding egg location (Fig. 3A), *thersites1* oviposited mainly on leaves (54%), followed by stems (31%) and flower buds (15%). *thersites2* also oviposited mainly on leaves (58%), followed by bracts (17%), grasses touching the host plant (17%) and stems (8%).

The two generations did not differ in egg locations ($\chi^2 = 7.64$, $df = 4$, $P = 0.11$). In *damon*, prevailing substrate were inflorescence bracts (84%), and *damon* differed highly significantly from both *thersites1* ($\chi^2 = 30.07$, $df = 3$, $P < 0.00001$) and *thersites2* ($\chi^2 = 24.06$, $df = 3$, $P < 0.0001$).

Regarding Sainfoin phenology (Fig. 3B), *P. thersites* generations expectably differed, as most of the plants used by *thersites1* were Not flowering yet, while those used by *thersites2* were mostly Fruiting ($\chi^2 = 25.0$, $df = 2$, $P < 0.00001$). On the other hand, *thersites2* females did not differ from *damon* females, both using mostly Fruiting plants for oviposition ($\chi^2 = 2.17$, $df = 2$, $P = 0.34$).

P. damon placed eggs to a higher height than both generations of *P. thersites* (Kruskal-Wallis: $H(2, 62) = 29.19$, $P < 0.00001$) (Fig. 3C). Sainfoin height was higher in *damon* than in *thersites1*, while *thersites2* was intermediate (Kruskal-Wallis: $H(2, N = 62) = 7.65$, $P < 0.03$) (Fig. 3D). Finally, surrounding Sward was higher in case of *damon* than in both *thersites1* and *thersites2* (Kruskal-Wallis test: $H(2, N = 62) = 16.79$, $P < 0.0002$) (Fig. 3E).

Landscape occupancy patterns

Out of the 54 sites surveyed, *P. thersites* occurred at 14 sites and *P. damon* at only four sites, forming two adjoining pairs. The sites hosting *P. damon* hosted *P. thersites* as well (Fig. 2; Appendix 1). One of the localities, Kamenny vrch, is described in Material and Methods: Oviposition patterns. Considerably smaller Černá hora adjoins Kamenný vrch grasslands at the South, the two sites are separated by ~ 100 m of arable land. Na Adamcích is a reserve of formerly grazed steppic grasslands situated on rolling loess slopes amidst intensively farmed landscape. The reserve is currently managed by hand mowing, following checkerboard-like manner. Nearby and much smaller Sovince reserve shares with

Table 1. Single-term GLM regressions of presence/abundance of *Polyommatus thersites* and *P. damon* against variables describing site topography, connectivity, habitats within site and site management.

	<i>Polyommatus thersites</i>				<i>Polyommatus damon</i>			
	Abundance		Presence		Abundance		Presence	
Null model	54.33		63.61		33.99		30.76	
Covariates								
Visits	48.54	↑*	43.18	↑****	23.98	↑**	27.31	↑*
<i>Geography variables</i>								
Altitude	56.68		65.78		35.88		32.20	
Longitude	50.71	↑*	65.23		36.63		29.06	
Latitude	53.96		65.64		34.49		30.90	
<i>Site conditions</i>								
Area	55.52		65.11		37.62		32.38	
Slope	55.36		64.22		28.36	↑**	28.94	
Orientation	54.22		65.46		36.38		32.24	
Sainfoin density	32.70	↑****	45.01	↑****	20.57	↑****	20.46	↑****
<i>Habitat type</i>								
Xeric grassland	53.11		59.34	↑*	13.30	↑****	15.54	↑****
Ruderal grassland	53.43		63.64		27.29	↓**	26.00	↓**
Abandoned orchard	56.67		63.80		36.94		29.93	
Woodland edges	56.68		65.79		34.44		31.48	
Terraces	52.67		62.40		36.57		26.65	
Field banks	54.67		64.86		33.82		29.65	
Clearings	54.23		65.15		37.67		32.20	
<i>Management</i>								
Mowing	41.60	↑↓**	48.54	↑↓***	21.86	↑↓****	22.49	↑↓***
Grazing	46.87	↑**	53.89	↑***	33.68		27.14	↑*
Neglect	39.43	↓↑***	46.69	↓↑***	11.54	↓↑****	13.83	↓↑****
<i>Relative site connectivity</i>								
Closest <i>thersites</i>	52.57		64.04		16.00	↑****	15.91	↑****
Closest <i>damon</i>	56.99		65.79		2.02	↑****	0.11	↑****
Three steppes	56.68		65.95		35.92		32.29	

Explanations: The values of AIC are stated, the darts indicate positive (↑), negative (↓) or polynomial (↑↓) response. ANOVA test against covariate model: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

the former vegetation and past land use, the two are separated by ~200 m of arable land and housing settlements.

In single-term regressions (Table 1) the probability of detection increased with Visits. *P. thersites* abundance increased with Longitude, i.e. towards the East. Sainfoin abundance affected both species (and both presence and abundance) positively. *P. damon* abundance also increased with Slope. Among habitat variables, the proportional representation of Xeric grassland affected both species positively (except *P. thersites* abundance), and that of Ruderal grassland affected *P. damon* (both presence and abundance) negatively. The presence and abundance of both species responded in a concave form to the proportional representation of Mowing and Neglect managements, with maxima corresponding to ca 80 per cent of site area mown, or 35 per cent of site area unmanaged. Grazing positively affected *P. damon* (presence), and *P. thersites* (presence, abundance). Finally, *P. damon* presence and abundance were positively affected by the distance to the closest sites occupied by either *P. thersites* or *P. damon* (Table 1).

Forcing the Visits to the models changed the re-

sults as follows (Table 2). The effect of Slope on *P. damon* abundance disappeared, there appeared a weak negative relationship between *P. thersites* presence and proportion of Field embankments, and the effect of Grazing on *P. damon* presence was lost.

Multiple regressions (Table 3) not considering the Visits suggested that *P. thersites* presence and abundance were positively associated with Sainfoin density and some proportion of Neglect within the sites. For *P. damon*, both presence and abundance were best modelled by proximity to other occupied sites, explaining over 90% of variation in the data. Disregarding this predictor during the variable selection returned a weaker model associating *P. damon* presence/abundance with a proportion of Xeric grassland and Neglect (presence only) and with a proportion of Xeric grassland and Slope in case of abundance.

In models containing Visits, *P. thersites* was still positively influenced by an intermediate proportion of Neglect and by Slope (presence only) and Neglect (abundance only) (Fig. 4). For *P. damon*, the strongest predictor was still the proximity to the Closest *damon*. Ignoring this predictor returned, for presence, a model indicating a domed response to Neglect, plus to a pro-

Table 2. Single-term GLM regressions (covariate model) of presence/abundance of *Polyommatus thersites* and *P. damon* against variables describing site topography, connectivity, habitats within site and site management.

	<i>Polyommatus thersites</i>				<i>Polyommatus damon</i>			
	Abundance		Presence		Abundance		Presence	
Covariate model ^{A)}	48.54	↑*	43.18	↑****	23.98	↑**	27.31	↑*
Site conditions								
Area	50.57		44.01		26.19		29.69	
Slope	51.33		44.40		24.53		28.90	
Orientation	50.67		41.47		26.74		30.33	
Sainfoin density	31.95	↑****	31.92	↑****	15.05	↑****	18.89	↑****
Habitat type								
Xeric grassland	50.53		40.50	↑*	10.36	↑****	14.44	↑****
Ruderal grassland	49.36		43.67		19.45	↑*	23.50	↑*
Abandoned orchard	51.11		43.73		24.60		28.24	
Woodland edges	46.08		44.78		23.90		27.38	
Terraces	47.98		42.79		25.18		28.68	
Field banks	49.12		39.70	↓*	22.89		26.51	
Clearings	47.49		43.26		25.79		29.30	
Management								
Mowing	37.49	↑↓**	25.07	↑↓****	16.57	↑↓**	22.28	↑↓*
Grazing	40.72	↑**	31.99	↑****	22.53		25.01	
Neglect	34.91	↓↑****	22.45	↓↑****	5.92	↓↑****	9.35	↓↑****
Relative site connectivity								
Closest <i>thersites</i>	45.79		43.50		10.13	↑****	13.48	↑****
Closest <i>damon</i>	51.27		44.85		0.53	↑****	0.10	↑****
Three steppes	50.88	h	44.92		31.45		31.85	

Explanations: The darts indicate positive (↑), negative (↓) or polynomial (↑↓) response. ANOVA tests against covariate model **P* < 0.05, ***P* < 0.01, ****P* < 0.001, *****P* < 0.0001. ^{A)} Visits was the only predictor entering all covariate models.

Table 3. Multiple regressions used to study effects of landscape and site predictors on presence and abundance of *Polyommatus thersites* and *P. damon* butterflies (GLM, Poisson distribution of abundance, binomial distribution for presence, forward selection of predictors).

<i>Polyommatus thersites</i>					<i>Polyommatus damon</i>				
Abundance					Abundance				
	<i>D</i> ²	AIC	df	<i>P</i>		<i>D</i> ²	AIC	df	<i>P</i>
Null model		52.98	53		Null model		31.98	53	
~Sainfoin density +(Neglect) ²	47.1	20.45	3, 50	***	~Closest <i>damon</i>	94.1	29.96	1, 52	***
					~Slope +(Neglect) ²	81.9	24.92	3, 50	***
					Presence				
Null model		62.44	53		Null model		28.52	53	
~Sainfoin density +(Neglect) ²	39.6	19.9	3, 50	***	~Closest <i>damon</i>	99.6	0.11	1, 52	***
					~Xeric grassland +(Neglect) ²	90.0	3.16	3, 50	***
					Abundance				
						<i>D</i> ²	AIC	df	<i>P</i>
					~Visits	16.33	46.30	1, 52	***
					~Visits +(Neglect) ²	44.26	28.81	3, 50	***
					~Visits	37.89	19.99	1, 52	***
					~Visits +Closest <i>damon</i>	98.50	0.53	2, 51	***
					~Visits +(Mowing) ² +(Neglect) ²	93.14	2.70	5, 48	***
					Presence				
					~Visits	36.03	40.82	1, 52	***
					~Visits +(Neglect) ² +Slope	76.10	17.95	4, 49	***
					~Visits	20.00	5.69	1, 52	***
					~Visits +Closest <i>damon</i>	99.63	0.10	2, 51	***
					~Visits +(Neglect) ² +Xeric grassland	80.77	3.21	4, 49	***

portional representation of Xeric grassland, suggesting that the best sites were the partly abandoned ones. For abundance, the model indicated domed responses to Mowing and Neglect, suggesting a requirement for diversified sites with both managed and unmanaged patches.

Discussion

Although both *Polyommatus thersites* and *P. damon* have declined substantially in the Czech Republic, and elsewhere in Central Europe, *P. damon* declined more severely. Comparing egg-laying patterns of the two

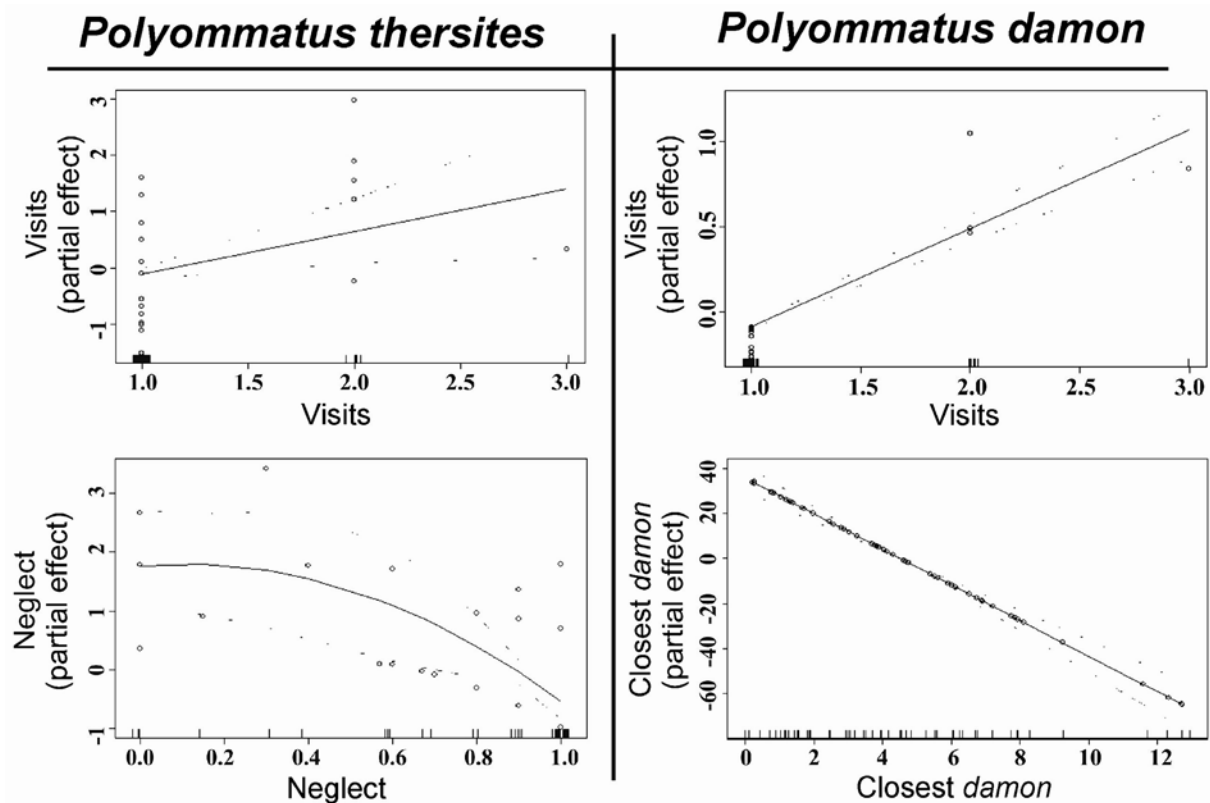


Fig. 4. Illustration of multiple regression models for abundance of *Polyommatus thersites* and *P. damon* butterflies on islets of xeric grasslands in southeastern Moravia, Czech Republic. The panels show partial effects of model terms Visits and Neglect (*P. thersites*), and Visits and Closest *damon* (*P. damon*) on local abundance of the butterflies, expressed on a 0–3 ranked scale.

species, and their habitat utilisation on a landscape scale, allows elucidating the mechanistic reasons behind their differing fates.

We detected differences in oviposition patterns between the two species, as well as between generations of *P. thersites*. Starting with the latter, spring *P. thersites* females utilised mainly leaves of unflowering sainfoin ramets, although a few plants were already blooming in time of their flight. Fresh plant parts, such as unfolded leaves, might be more nutritious for larvae (Forister 2005), but this should not apply for short-lived herbs (Čížek et al. 2006). We did not quantify the relative supply of host plant parts available to spring and summer *P. thersites* generations, however, and hence cannot decide whether oviposition on the leaves reflected a genuine preference, or the availability of host plant parts. More notable were the differences between *P. damon* and summer generation of *P. thersites*. While summer *P. thersites* females still oviposited mainly on leaves, *P. damon* females laid eggs on sainfoin bracts. Consequently, *P. damon* eggs were placed at higher heights, although the heights of host plants themselves did not differ between *P. damon* and summer-generation *P. thersites*.

These patterns suggest that *P. damon* eggs and larvae are more vulnerable to management actions than those of *P. thersites*. Mowing in high summer (July – August), which is the most common conservation management currently in use at Moravian xeric grasslands, destroys sainfoin flowerheads, including *P. damon* eggs

if already laid. It also prevents sainfoin plants to resprout into bloom, so that *P. damon* females suffer shortages of egg-laying substrates. None of these risks affect *P. thersites*, whose eggs are hidden low in the sward and whose larvae feed on leaves, rapidly resprouting after mowing. Notably, *P. thersites* is still persisting at numerous sites in Poland, from which *P. damon* disappeared several decades ago (Buszko & Maslowski 2008).

The historical management of south Moravian xeric grasslands combined grazing by all kinds of animals with mowing, according to momentary needs of the farmers. Considering *P. damon* life history, summer grazing appears as destructive as summer mowing, and perhaps even more so, given that sheep preferentially consume legumes' flowerheads. Earlier it was observed (Kudrna 1998), that sheep grazing rapidly exterminated a population of *P. damon* in the Rhön Mts., Bavaria and several authors have discussed this (Beneš et al. 2002; Nässig et al. 2004). Shortly before 2000, reestablishment of sheep grazing as a reserve management method extirpated *P. damon* from at least one Czech reserve (Rašovický zlom reserve), while mowing in high summer extirpated it from another one (Strabišov-Oulehla reserve) (Beneš et al. 2002, and subsequent observations by the authors). On the other hand, entire *P. damon* distribution in north-western Bohemia (cf. Figure 1) is restricted to three small (< 1 ha each) colonies, but the species has persisted there for at least 20 years, apparently owing to exclu-

sion of sheep grazing (see Kadlec et al. 2009 for details on the Bohemian sites).

Grazing later in autumn may be less destructive than grazing in summer. At a locality in Frankonian Jura, Bavaria, Dolek (1994) observed that over 80% of larvae hatched by late September left the inflorescences and fed on sainfoin leaves near the ground. Consequently, Dolek & Geyer (2002) recommended autumn grazing for Frankonian Jura xeric grasslands, provided that it is practised patchily, not affecting entire grassland patches.

A further reason behind the faster *P. damon* decline may be its univoltine development, contrasting to the bivoltine development in *P. thersites*. Having more generations per year should allow species to build up higher local densities in the course of vegetation season. This may represent a bet-hedging strategy, especially if the more abundant generation exhibits increased mobility (cf. Fric et al. 2006). This consideration does not apply in an absolute manner, however. *Polyommatus coridon* (Poda, 1761) and *P. bellargus* (Rottemburg, 1775) represent a pair of lycaenid butterflies sharing an identical host plant, in which the former one is univoltine and fares quite well across Western Europe, whereas the latter is bivoltine and declining (cf. Bourn & Thomas 2002; Brereton et al. 2008). Roy & Thomas (2003) reported that *P. bellargus* requires more diversified sward and microclimatic conditions to meet larval development needs during two climatically different periods of the year, high summer and early spring.

Patterns of landscape occupancy corroborated the higher sensitivity of *P. damon*. The results must be viewed with reservations, however, because only four of the 54 sites surveyed were occupied by *P. damon*, rendering any inference rather spurious. Still, we found that both butterflies required sites with high host plant density, quite expectably in monophagous species (e.g., Krauss et al. 2004; Rosin et al. 2011; Roy & Thomas 2003), and both tended to occur at sites with variable management. *P. thersites*, but not *P. damon*, also increased with proportional representation of grazing, in accordance with our oviposition patterns observations. The need for heterogeneous grassland reserves management has been advocated since the 1970s (Morris 1967). Given that such reserves constitute islets carved from originally heterogeneous landscapes, managers should not only mimic traditional management of a particular site, but should attempt to pack into each site as much as possible a diversity of conditions historically existing in wider environs (Čížek L. et al. 2012; Konvička et al. 2005; Morris 2000; Settele et al. 2009). Each management action accelerates insect mortality (Čížek O. et al. 2012; Dover et al. 2010), either directly, or by depriving the insects of food or shelter (cf. Dennis et al. 2003). Failures to diversify reserve management can decrease local populations and contribute to the extinction of butterfly species (Konvička et al. 2008; Schtickzelle et al. 2007).

Presence of *P. damon*, but not *P. thersites*, was strongly affected by the proximity to the nearest occu-

pled sites, and this effect overrode any effects of site management in regression models. Strong effect of connectivity on site occupancy patterns is often assumed to indicate a metapopulation dynamics, in which local extinctions are compensated by recolonisation processes (Hanski 1999). Existence of such effect on site occupancy of another small-sized lycaenid, *Cupido minimus* (Fuessly, 1775) was interpreted in terms of the species' dispersal ability (Binzenhofer et al. 2008; Krauss et al. 2004). In our case, the absence of effect on *P. thersites* might be interpreted in two ways. Either no metapopulation processes apply here so that the occupied sites represent self-sustaining populations (perhaps with metapopulation processes within the sites: Thomas et al. 2002), or, less likely, all the studied sites are within the reach of dispersing individuals. In *P. damon*, in contrast, only sites adjoining other occupied sites were occupied. *P. damon* is hence surviving only at sites that are large enough to sustain a population and in the same time appropriately managed. Near such refuge sites (Na Adamčích, Kamenný vrch: see Appendix 1), it forms smaller satellite colonies (Černá hora, Sovince). A few other unoccupied but potentially inhabitable sites with high sainfoin density exist (e.g., Pouzdřanská step, Horky: Appendix 1), but are too far for spontaneous colonisation.

P. damon and *P. thersites* represent a pair of co-occurring species, in which *P. damon* is more sensitive to host plant conditions, and hence habitat management. Similar situations, besides the above *P. coridon* and *P. bellargus* example, apply for European lycaenids *Phengaris teleius* (Bergsträsser, 1779) and *P. nausithous* (Bergsträsser, 1779), in which the former requires a more abundant host plant (Dierks & Fischer 2009); South African lycaenids *Orachrysops ariadne* (Butler, 1898) and *O. subravus* (Henning & Henning, 1994), which occur sympatrically but the latter utilises a more common host plant and displays less efficient dispersal (Samways & Lu 2007); or the Californian checkerspots *Euphydryas editha bayensis* (Sternitzky, 1937) and *E. chalcedona* (Doubleday, 1847) the former displaying a higher habitat specificity (Murphy et al. 1986). In such cases, insensitive management can considerably weaken the populations of the more sensitive species, particularly so in highly fragmented landscapes with a restricted supply of inhabitable sites.

Management of shared *P. thersites* and *P. damon* sites must respect the more sensitive species, *P. damon*. Mowing or grazing, although necessary to block succession (Bourn & Thomas 2002), must be applied with utmost care. Rather than affecting the entire site, about a third of a locality can be cut or grazed each year, which should suffice to prevent succession while maintaining enough sainfoin to fruit. Because the plant tends to be distributed patchily, management should proceed in a checkerboard-like manner. If grazing is applied, it should strictly avoid the period when it would impair the *P. damon* life cycle, i.e., June – September.

An appropriate management of occupied sites should be accompanied with effort to enhance the num-

ber of colonies, by both restoring sainfoin at appropriate sites near the currently occupied ones, and by reintroducing the butterfly to vacant but suitable sites. In warm parts of Central Europe, *Onobrychis vicifolia* was grown as a fodder and bee plant in the past and there are anecdotal records of *P. damon* occurring at sainfoin fields (Schwarz 1948). It is highly desirable to re-establish the plant at such localities as warm road verges, nonintensive field margins sustained under the Agro-environmental schemes, or at biologically-treated vineyards. Laudable attempts in this direction are underway: sainfoin is included to flower-rich mixtures for highway verges greening (Konvička et al. 2005) and biological vineyards (Hluchý 2011). Targeting these actions to the proximity of current *P. damon* sites might considerably increase *P. damon* chances for survival.

To summarise, our study illustrates the utility of detailed life history knowledge for conserving declining butterflies of xeric grasslands, as well as the necessity of mosaic-like, patchy management of grassland reserves. Packing diverse vegetation management approaches into standing reserves may at least partially substitute for the lost habitat diversity of farmland landscapes, and hence to assist future recovery of currently endangered species.

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Appendix 1. List of all xeric grassland patches visited and their main characteristics.

Name	Reserve	Number of visits	Area [ha]	Altitude	Latitude	Longitude	Presence		Host plant density
							<i>P. thersites</i>	<i>P. damon</i>	
Bažantnice	–	1	18.2	278	48°57'57.6"	16°45'46.8"	1	0	1
Čaušperky	–	1	0.15	293	48°57'29.8"	16°47'46.6"	0	0	0
Černá hora	+	2	3.85	304	48°57'46.8"	16°45'10.8"	1	1	2
Díly	–	1	1.48	216	48°57'57.6"	16°52'44.4"	0	0	0
Diváky	–	1	1.84	253	48°59'31.2"	16°46'58.8"	0	0	0
Hájek	–	1	3.14	285	48°57'20.5"	16°48'7.018"	0	0	2
Hájenka	–	1	0.22	260	48°57'33.3"	16°51'31.4"	0	0	0
Horky	+	1	15.5	236	48°56'34.5"	17°8'3.1"	1	0	2
Hradisko	–	1	0.22	254	48°57'43.2"	16°45'46.8"	0	0	0
Hrubé odměry	–	1	0.27	232	48°56'34.8"	16°50'6.0"	0	0	0
Hustopečský rybník	–	1	5.24	225	48°57'43.2"	16°44'20.4"	0	0	0
Jesličky I	+	1	1.34	235	48°56'33.8"	16°50'21.7"	0	0	1
Jesličky II	+	1	1.1	247	48°56'33.8"	16°50'35.0"	0	0	0
Kamenný vrch	+	3	65.0	301	48°57'56.0"	16°45'12.0"	1	1	2
Keramička	–	1	1.14	184	48°59'24.0"	16°54'57.6"	0	0	0
Klínky	–	1	2.5	237	48°33'36.0"	16°28'12.0"	0	0	0
Kněžské za humny	–	2	0.19	276	48°56'27.6"	16°49'12.0"	1	0	2
Kroužky	–	2	3.28	263	48°57'34.6"	16°51'44.7"	1	0	1
Kurdějovska	–	1	4.81	262	48°55'58.8"	16°47'16.8"	0	0	0
Kurdějovský rybník	+	2	0.73	196	48°55'58.8"	16°46'58.8"	1	0	1
Lipiny	+	2	14.3	317	48°58'9.7"	16°46'13.8"	1	0	2
Louky pod Kumstátem I	+	1	1.44	198	48°59'36.3"	16°55'20.3"	0	0	2
Louky pod Kumstátem II	+	2	0.81	217	48°59'45.1"	16°55'15.3"	1	0	2
Maňásek	–	1	0.31	257	48°59'49.2"	16°49'15.6"	0	0	0
Na Adamcích	+	1	7.5	273	49°0'14.4"	16°59'56.4"	1	1	2
Němčičky	–	1	0.19	288	48°56'13.2"	16°48'54.0"	0	0	2
Odměry	–	1	0.05	275	48°56'45.6"	16°49'51.6"	0	0	0
Paseky	–	1	5.7	200	48°57'54.0"	16°48'57.6"	0	0	2
Pod klínky	+	1	3.4	210	48°55'58.8"	16°47'56.4"	1	0	1
Pod padělký	–	1	0.98	243	48°59'42.0"	16°46'51.6"	0	0	0
Pouzdranská step	+	1	10.17	268	48°33'36.0"	16°22'47.6"	1	0	2
Přední Boří	–	1	0.74	289	48°58'58.8"	16°46'11.6"	0	0	0
Přední kout	+	1	1.52	383	48°58'19.2"	16°45'57.6"	0	0	2
Přestavky	–	1	3.27	229	48°57'57.6"	16°50'42.0"	0	0	0
Pustna	–	1	0.36	324	48°59'38.4"	16°45'32.4"	0	0	2
Roháče	–	1	0.84	251	48°55'51.6"	16°47'45.6"	0	0	0
Sad u Nikolčic	–	1	4.63	347	48°59'19.9"	16°46'40.1"	0	0	0
Sádky	+	1	1.34	273	48°57'0.0"	16°46'15.6"	1	0	2
Sovince	+	1	0.85	228	49°0'28.8"	17°0'32.4"	1	1	2
Step u Lipin I	+	1	1.65	306	48°57'46.8"	16°46'19.2"	0	0	2
Step u Lipin II	+	1	5.9	305	48°57'57.6"	16°46'30.0"	0	0	1
Step u Lipin III	+	1	0.61	306	48°57'57.6"	16°46'30.0"	0	0	0
Stračí	+	1	3.4	260	48°56'24.0"	16°48'57.6"	0	0	1
Štřelnice	+	1	11.34	328	48°57'0.0"	16°43'48"	0	0	2
Šneholec	–	1	3.9	240	48°58'22.8"	16°48'54"	0	0	0
Štěpnice	–	1	10.24	246	48°55'58.8"	16°46'58.8"	0	0	0
Štumperk	–	1	4.75	283	48°57'23.3"	16°47'46.2"	0	0	0
Terasy u Nikolčic	–	1	18.5	290	48°58'48.9"	16°44'42.3"	0	0	0
Topolany	–	1	0.36	204	48°57'32.4"	16°50'49.2"	0	0	0
U cihelny	–	1	2.3	244	48°59'52.8"	16°48'57.6"	0	0	1
Vlčí dolina	–	1	0.89	243	48°58'26.4"	16°44'24.0"	0	0	0
Závisté	–	1	57.53	352	48°58'58.8"	16°48'58.6"	0	0	1
Žabí mez	–	1	3.6	252	48°57'25.2"	16°51'0.0"	0	0	0
Ždánice	–	1	2.4	286	49°0'43.2"	17°0'0.0"	0	0	0