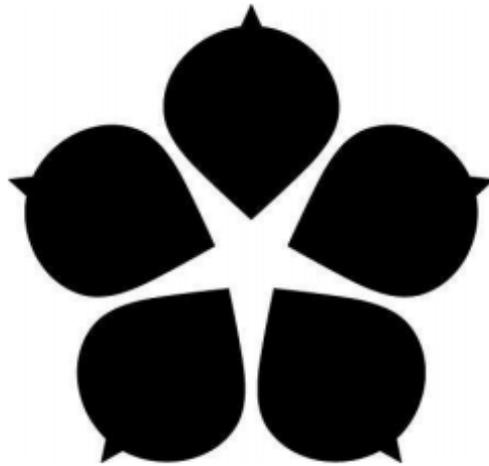


University of South Bohemia in České Budějovice

Faculty of Science



**Will refaunation by feral horse affect five
checkerspot butterfly species (*Melitaea* Fabricius,
1807) coexisting at xeric grasslands of Podyji
National Park, Czech Republic?**

RNDr. Thesis

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Annotation

This thesis focuses on the population structure of five fritillary butterfly species – *Melitaea athalia*, *M. cinxia*, *M. didyma*, *M. britomartis* and *M. aurelia* – co-occurring on two xeric grassland localities of the Podyjí National Park, Czech Republic – Havranické vřesoviště and Mašovická střelnice. Recently, both of these sites are threatened by succession and degradation processes. Due to that, they have been chosen for whole season grazing by a large herbivore (Exmoor pony). This study describes adult demography structure, adult mobility and adult habitat requirements of the five butterflies prior to the grazing management establishment.

Prohlašuji, že jsem autorem této kvalifikační práce a že jsem ji vypracoval(a) pouze s použitím pramenů a literatury uvedených v seznamu použitých zdrojů.

České Budějovice, 14.4.2021

Vodičková Veronika

Contribution of the candidate

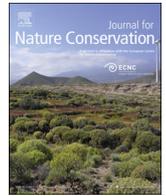
The thesis is based on the attached publication, which is based on my bachelor thesis. Together with my supervisor, I designed the study, carried out at ca 30% of data collection in the field, managed the collected data, performed ca 50% of data analyses, and jointly with my supervisor wrote the paper.

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Will refaunation by feral horse affect five checkerspot butterfly species (*Melitaea* Fabricius, 1807) coexisting at xeric grasslands of Podyji National Park, Czech Republic?

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ABSTRACT

In connection with the broad refaunation/rewilding movement, free-range grazing by native ungulates is being increasingly used as a management option for diverse habitat types, including xeric grasslands of temperate Europe. Prior to the establishment of such grazing by Exmoor ponies, an analogue of the wild horse for European grasslands, we surveyed the demography, mobility and habitat use of five species of checkerspot butterflies (*Melitaeini*) co-occurring at two grasslands of the Podyjí National Park, Czech Republic: *Melitaea athalia*; *M. aurelia*; *M. britomartis*; *M. cinxia*; and, *M. didyma*. We combined mark-recapture, adults distribution models and larval nests surveys to describe co-occurrence patterns of the five butterflies and to predict impacts of the horses on their populations.

All five species co-occurred at grassland M, a former military training range. *M. aurelia* and *M. britomartis* were absent from grassland H, a former village commons, the latter due to a recent local extinction. Four species conformed to adult demography patterns typical for univoltine *Melitaeini*, while *M. didyma* formed multiple generations. Mobility inversely reflected current distribution ranges in the Czech Republic: the widespread *M. athalia* and *M. cinxia* were most mobile, the currently expanding *M. didyma* was intermediate, and the range-restricted and endangered *M. britomartis* and *M. aurelia* were least mobile. Habitat requirements followed a gradient from wooded structures (*M. athalia*), through long-sward shrubby sites (*M. britomartis*), short-sward grasslands (*M. cinxia*) to open-turf sites (*M. aurelia*, *M. didyma*).

Based on our findings, we predict that natural grazing by the ponies will benefit *M. aurelia*, *M. cinxia* and *M. didyma*, and will be neutral for *M. athalia*. It may pose a risk for *M. britomartis*, rather an open woodlands dweller, which likely benefited from successional overgrowth of the grasslands. As its conservation is a top priority, we recommend measures to mitigate the negative impacts.

1. Introduction

Temperate xeric grasslands, including their transitions to scrub and wooded meadows, represent the most rapidly declining land form both globally and in Central Europe (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Torok, Ambarli, Kamp, Wesche, & Dengler, 2016). Often restricted to rather unproductive soils and maintained for millennia by human activities such as hay-making or grazing, xeric grasslands host diverse and highly specialised insect assemblages, including relics of early Holocene, or even earlier, conditions (Dengler, Janisova, Torok, & Wellstein, 2014; Poschlod & Wallis de Vries, 2002). Much of the pre-industrial extent of such grasslands has been lost to development,

afforestation, or post-abandonment succession (Forejt et al., 2017). The remaining fragments are mostly legally protected (cf. Slancarova, Benes, Kristynek, Kepka, & Konvicka, 2014) and painstakingly managed by mimicking pre-industrial land uses (Bonari et al., 2017; Talle et al., 2016). In connection with the recent refaunation/rewilding movement (Seddon, Griffiths, Soorae, & Armstrong, 2014; Svenning et al., 2016), free-range grazing by native large ungulates is increasingly advocated as a management option (e.g., Bokdam & Gleichman, 2000; Jirku and Dostal, 2015; Merckx & Pereira, 2015; Henning, Lorenz, Von Oheimb, Haerdte, & Tischew, 2017). This is an outcome of a radical shift in the perception of the role of large herbivores in temperate ecosystems' natural dynamics (Bocherens, Hofman-Kamińska, Drucker, Schmöcke,

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& Kowalczyk, 2015; Galetti et al., 2018; Vera, 2000). Contrary to earlier views that under “wild” conditions, large ungulates would live in low densities within close-canopy woodlands, it is now understood that they would be rather abundant, keeping temperate landscapes in a state of shifting grassland-woodland mosaics (Johnson, 2009; Sandom, Ejrnæs, Hansen, & Svenning, 2014). What for long have been perceived as seminatural (or “cultural”) grasslands may instead represent the most ancient biotopes of Central Europe (Feurdean, Ruprecht, Molnár, Hutchinson, & Hickler, 2018).

With the increasing number of sites grazed, or considered for grazing, by wild ungulates (or ancient domestic breeds as analogues) across Europe, there is increasing demand for studying the effects on associated biota (van Klink, van der Plas, van Noordwijk, WallisDeVries, & Olf, 2015; van Klink & WallisDeVries, 2018). Managers should not rely on the simplistic belief that since grassland biota had evolved in a megafaunal world, they would automatically benefit from the return of megafaunal ungulates. Compared to pre-cultural landscapes, modern landscapes are severely fragmented, populations of many organisms diminished, and the scale of most “rewilding” projects too small to blindly rely on an automatic establishment of beneficial processes (van Klink & WallisDeVries, 2018). Wherever the grazing aims to benefit rare and declining species, which is mostly the case, requirements of such species should be studied in advance, and the projects should be pre-adapted to minimise potential harm. This, of course, does not exclude the need for follow-up monitoring of the intervention outcomes.

Southern Moravia, SE Czech Republic (hereinafter “CZ”), is an intensively farmed low-elevated region, where xeric grasslands persist as small actively managed remnants (Cizek, Hauck, & Pokluda, 2012; Slancarova et al., 2014). Free-range grazing by a primitive horse breed, the Exmoor pony, has been established in 2018 at two such grasslands in the Podyjí National Park. With five co-occurring species, the sites represent a national hotspot for checkerspot (*Melitaeini*) butterflies. These five species differ in conservation status, from widespread and not threatened in the country to critically endangered, and for at least one of them, *Melitaea britomartis* (Assmann, 1847), the park’s grasslands represent the only larger-sized site in the country (Benes & Konvicka, 2002). From a wealth of available information on this butterfly model group (Ehrlich & Hanski, 2004; Hanski, 1999), it can be reasoned that despite some overlaps in resource use explicable by close phyletic relatedness, the species will differ in habitat requirements, and hence respond differently to management interventions. For conservation risk assessment, a knowledge of basic demography parameters such as population size, spatial distribution and dispersal is necessary. For checkerspots, such information is rather conveniently obtained using mark-recapture (Ehrlich, 1965; Wahlberg, Klemetti, Selonen, & Hanski, 2002; Zimmermann, Blazkova et al., 2011; Zimmermann, Fric et al., 2011) and mapping communal larval nests (Hanski et al., 2017; Ojanen, Nieminen, Meyke, Poyry, & Hanski, 2013).

This paper reports the results of a detailed mark-recapture study of the five checkerspots, carried out a season before the establishment of the Exmoor ponies, with the principal aim of advising on the pros and cons of the imminent feral horses’ establishment. We followed the butterflies for their combined adult seasons, and used information on spatial positions of captures to discern which sections of the localities, and which resources, as indicated by vegetation structures, are essential for their existence. We 1) report on the basic adult demography characteristics for the five species prior to the establishment of the grazing, 2) describe their mobility patterns, 3) map the adult habitat use in relation to vegetation and the current conservation management, and 4) provide a basic description of larval habitats for two species with gregarious larvae. We hypothesize that abundances of the populations will roughly reflect the available areas of suitable vegetation structures, that mobility patterns will reflect the distribution of the species in a wider area, and that individual species will display attachment to particular vegetation type/succession stage. We use this information to predict

reactions of the system to the establishment of Exmoor ponies.

2. Material and methods

2.1. Study area

The transborder (CZ/Austria) Podyjí/Thayatal National Park protects an undeveloped and largely forested canyon of the Dyje/Thaya river at a contact zone between the cold and humid Hercynian highlands (West) and the warm and dry Pannonian lowlands (East). The two study sites are located at the canyon’s upper rims, on acidic granite bedrock.

Havraníky Heath (hereinafter “H”, 48.81 N, 16.00E, mid altitude 320 m, ≈1500 ha). Former village commons at the southwestern canyon rim. The mildly undulated south-oriented slopes form a transition between contiguous woodlands and intensive farmlands. Covered by a mosaic of grasslands, scrub (*Crataegus* spp., *Rosa* spp., *Cornus mas* and *C. sanguinea*), woodlots (oaks, hornbeam, *Pinus sylvestris*, and invasive *Robinia pseudoacacia*) and mesic meadows. Heather (*Calluna vulgaris*), once a prominent plant promoted by frequent fires (Sedlakova & Chytrý, 1999), has receded due to nutrient accumulation and is increasingly replaced by expansive grasses (*Arrhenatherum elatius*, *Calamagrostis epigejos*). To mimic traditional land use, the area has been managed by rotational sheep grazing, and by mechanical means such as scrub removal.

Mašovická Range (hereinafter “M”, 48.50 N, 15.58 E, altitude 400 m, ≈750 ha) A former military training ground, established in the 1950s and used by the army until the mid-1990s; it adjoins the canyon northeasterly, the relief is flat. The vegetation is similar, but more mesic than in H. An important feature are plentiful ditches and earth walls of varying length, width and orientation, created by the military and hosting rich flora owing to steep environmental gradients. The post-military management has ranged from ordinary machine mowing of more mesic and flat sections, through horse and sheep grazing, to neglect.

Both grasslands are exceptionally rich in butterfly and other insect groups species. A decade ago, butterfly surveys detected 62 (H) and 63 (M) species, ≈45% of the Czech Republic total (Bartonova, Benes, Fric, Chobot, & Konvicka, 2016; Cizek et al., 2013). Even more species occurred there historically (Sumpich, 2011).

2.2. Species studied

The following five checkerspots were recorded from the sites shortly prior to this study. The life history information follows Macek, Lastuvka, Benes, and Traxler (2015); the distribution in CZ follows Benes and Konvicka (2002) and subsequent records (see Supplementary material I); and CZ Red-list status Hejda et al. (2017).

***Melitaea athalia* (Rottemburg, 1775)**. 400 occupied CZ 10.5 x 11 km grid squares (87% of the country total), not threatened. A Palaearctic species distributed from Britain through Europe, Turkey and most of Northern Asia to Japan. Its habitats include woodland mantles, clearings and wooded meadows. In addition to a spring generation (late May–July), a partial autumn brood may occur in warm years. Larvae start feeding communally, but soon disperse and overwinter solitarily. The wide range of reported host plants include *Plantago lanceolata*, *Melampyrum* spp., *Euphrasia* spp. and *Veronica chamaedrys*. Studied in detail in Britain (Warren, 1987a, 1987b). In the recent past, known from H and M sites.

***M. aurelia* (Nickerl, 1850)**. 39 CZ squares (8.5%); critically endangered. A West-Palaearctic species, ranging from eastern France across Central Europe and the Balkans through European Russia to the Tian-Shan Mts. It is associated with rocky outcrops, steppe grasslands and forest-steppes. Adults form a single annual brood (June–July), larvae feed communally on *Plantago* spp. (mainly *P. media*), *Veronica* spp. and *Melampyrum* spp. Overwintering is communal, the larvae

disperse in spring. It has been studied in detail in Germany (Eichel & Fartmann, 2008; Habel, Meyer, & Schmitt, 2009) and South Moravia (Novotny, Konvicka, & Fric, 2012). Known from M only.

M. britomartis (Assmann, 1847). Seven CZ squares (1.5%); critically endangered. A Euro-Siberian species ranging from Central Europe to the Amur region; in Central Europe from Germany and SE Poland to the Balkan peninsula (extinct in NE Italy: Cerrato, Bonelli, Loglisci, & Ballieto, 2014). It inhabits damp grasslands, sparse woodland and woodland-grassland transitions, including coppices. A single adult brood occurs in June–July. Host plants in Europe include *Veronica teucrium* and *V.* (= *Pseudolysimachion spicatum*, the larvae develop communally. Batori, Pecsénye, Bereczki, and Varga (2012) have studied its population genetic structure in Hungary. Previously known from both H + M.

M. cinxia (Linnaeus, 1758). 82 CZ squares (18%); endangered. A Palaearctic species distributed from the British Isles to the Far East, in Europe from southern Fennoscandia to the Mediterranean region. Inhabitant of nutrient-poor dry grasslands, forming a single adult generation (May–June). Communal larval development on *Plantago* spp. (mainly *P. lanceolata*) and several *Veronica* spp. Studied in detail in Northern Europe (e.g., Ahola, Wahlberg, & Frilander, 2017; Hanski et al., 2017; Saccheri et al., 1998), less elsewhere (e.g., Curtis & Isaac, 2015; van Noordwijk, Flierman, Remke, WallisDeVries, & Berg, 2012). Known from H + M.

M. didyma (Esper, 1779). 31 CZ squares (6.7%); endangered. A West-Palaearctic species, distributed from N Africa through Europe up to C Asia, Mongolia and Central Siberia. Inhabitant of xeric grasslands of various types, forming a single brood (June–August) in more northerly areas, but multiple broods in the south. Larval hosts include *Verbascum* spp., *Plantago lanceolata* and *Linaria* spp. Molecular genetic studies from Germany, near the species' northern limits, disclosed surprisingly efficient dispersal ability (Johannesen, Veith, & Seitz, 1996). Known from H + M.

2.3. Mark-recapture

The marking proceeded between 16 May and 29 July 2017. Each day with suitable weather, 1–3 persons explored both sites in a systematic manner approximately from 10:00 to 17:00 (CEST), marking as many individuals as possible. It took 2–3 consecutive days to cover the entire areas of both sites. The butterflies were marked by unique codes, combining letters (denoting the researcher and locality) and serial numbers. At each capture, we recorded: species, sex, date, closest hour, and wing wear (1–4, fresh to heavily worn). Each capture point, denoted by the butterfly code and time, was immediately drawn into a 1:8000 printed aerial photograph (≈ 5 m precision), new photographs were used for each marking day.

2.4. Adult demography

Separately for each species \times sex \times site combination (herein “system”), demography parameters were estimated using POPAN parametrisation of the Jolly-Seber model for open populations in MARK v. 8.2. (White & Burnham, 2009). The program fits a 1/0 matrix of successive captures models differing in complexity, selecting the most parsimonious model(s) using the information theory approach (Akaike, 1974).

The three primary parameters are: apparent survival ϕ ; capture probability p ; and proportional recruitment $pent$. They may be constant (\bullet), sex- (g) or time-dependent; the time effects may be factorial (t), linear (T), quadratic (T^2) or cubic (T^3) with respect to marking day. Time and sex may interact additively or multiplicatively. The derived parameters are daily recruitment B_i , daily population N_i and total population size N' (details: Schtickzelle et al., 2002; Zimmermann, Blazkova et al., 2011).

To obtain constant values ϕ_{con} and p_{con} for comparisons across

systems, we constructed models, derived from those with the lowest $qAIC$ (quasi-Akaike information criterion) values, by setting the parameter in question constant. Average longevity (in days) is obtained as $-\ln \phi_{con}^{-1}$.

To explore patterns of adult phenology and ageing, we regressed, separately for each system, wing wears recorded for all capture events in a given day against the serial number of the day (the first capture for a given system = day 1) and compared the resulting regression slopes (Ehl, Holzhauser, Ryrholm, & Schmitt, 2019).

2.5. Mobility

All the capture points were digitized using ArcGIS v. 10.5.1; attributes were code, date, time, species and sex. The total number of captures per individual (C) and total time elapsed between consecutive captures (Hr) were covariates in subsequent analyses, because movement distances increase with time elapsed. We then obtained three basic parameters per individual: total flight distance (= TFD , summed across consecutive capture points); longest single move (LSM); and mean flight distance ($MFD = TFD / C$).

We compared the three parameters with respect to sex, site and species, using generalised linear models (\log_{10} -transformed responses, identity link). We used AIC values to compare models, considering those with $\Delta AIC \leq 2.0$ as equivalent. We always first constructed a covariate model, based on C , Hr and their interaction, and then modelled partial effects of predictors.

Further, we fitted the total flight distances crossed by individuals, separately for the systems, to the inverse power (IPF), a scale-invariant dispersal kernel function robust to variation in marking effort (Fric & Konvicka, 2007; Hill, Thomas, & Lewis, 1996): $P_{IPF} = \alpha D^{-n}$. The parameters α , and n are estimated by regressing the natural logarithms of the inverse cumulative proportions of individuals crossing given distances ($\ln P$) on the natural logarithms of distances: $\ln(P_{IPF}) = \ln(\alpha) - n \ln(D)$. We subsequently compared slopes of the fitted functions (Zar, 2009).

2.6. Adult habitat requirements

To analyse the distribution of adults within habitats, we used ArcGIS 10.5.1 (Environmental Systems Research Institute, Redlands, CA.) to vectorise two polygonal levels, *land uses* and *land covers*. *Land uses* were: road; swamp; sheep-grazed grassland; sheep-grazed orchard; horse-grazed grassland; water hole; mown grassland; mown orchard; neglected grassland; earth walls; arable field. *Land covers* were: barren (incl. short sward up to ≈ 15 cm); mid-sward (\approx knee-height); tall sward (\approx waist-height); short scrub (≤ 1.5 m); tall scrub (≥ 1.5 m); solitary trees; contiguous woodlots; rocks; arable; and, wetland.

We performed a topological check of the data to remove minor inaccuracies, overlaps and other errors. Then we carried out the intersection of the layers of land covers, land uses and layers with capture points. Around each capture point, we created circular buffers of 20 m and 50 m diameters and created a table of individual butterfly codes and the representation of land cover and land use categories within these buffers. The final data table for adult requirements analysis consisted of 10,220 lines, each referring to a single capture event.

These data were analysed in CANOCO 5.00, using the redundancy analysis (RDA), a linear multivariate ordination method (Ter Braak & Šmilauer, 2012). *Land covers* and *land uses* were the dependent multivariate variables, whereas butterfly species were factorial predictors. For each of the two buffers, we computed four models, explaining the distribution of butterfly individuals by *land covers*, *land uses*, *land covers* with *land uses* as covariables, and vice versa. Significance of the ordinations was Monte-Carlo tested (999 permutations).

2.7. Larval requirements

We focused on three species with communal larvae: *M. aurelia*; and *M. britomartis* and, *M. cinxia*. From 22–24 August 2017, we established 5 m diameter targeted plots, both at sites where we frequently encountered females during the marking (H: 23, M: 17) and at randomly generated points (H: 50, M: 55). At both targeted and random plots, we counted larval groups, if present. We then recorded: the plots' x- and y-coordinates, percentage cover of all possible host plant species, and percentage ground projections of trees (> 3 m height), short shrubs (1–2 m), tall shrubs (2–3 m), short herbs (< 0.75 m) and tall herbs (0.75–1.5 m) layers, and barren ground. We also recorded inclination and exposure to sun (the latter using 1–5 scale, with 1 for N and NE, 3 for flat terrains and 5 for S and SW), and ditch or road/path presence (categorical 1/0 variables). For each larval group detected, we recorded the host plant species, aboveground nest height, average height of the vegetation within a 0.5 m diameter circle centred by the nest, and the percentage covers of bare ground, forbs and grasses within that circle.

We analysed the data using RDA in CANOCO, with presence/absence of larval nests per plot as response variable. We first defined a spatial model, forward-selected from x- and y-coordinates and interactions. We then used CANOCO forward selection to define the best set of variables describing larval habitats of the studied checkerspot species.

2.8. Wider landscape occupancy

In 2018, i.e. the year after the mark-recapture work, we conducted three expedition surveys (11–13 May, 19–21 June, 15–18 July) to eight additional steppe grassland patches in a wider vicinity (< 5 km) of our focal sites, in order to ascertain the distribution of our study species in a wider landscape.

3. Results

3.1. Adult demography

We marked 8515 butterflies: 1498 in H (*M. cinxia*, *M. athalia* and *M. didyma*); and, 7017 in M (all five species) (Table 1). In H, *M. cinxia* ($n = 1,171$, sexes combined) was most frequently marked, followed by *M. didyma* (242) and *M. athalia* (85). In M, the ranking was *M. aurelia* (2726), *M. britomartis* (2277), *M. athalia* (1322), *M. cinxia* (652) and *M. didyma* (40). The percentages of recaptures were highest for the least

abundant *M. didyma* (both sites $\approx 30\%$, sexes combined), followed by *M. cinxia*, M (28%). The percentages were much lower for the remaining species (10–14%). Across systems ($n = 16$), they did not correlate with marked, recaptured, or capture events numbers (Spearman's r , all $P > 0.15$). Within species, $\sigma\sigma$ were recaptured more frequently than ♀♀ , except for *M. aurelia* M, with near-identical recaptures (13.3% vs. 13.6%).

Phenologically (Table 1, Fig. 2), flight of *M. cinxia* and *M. athalia*, two species that co-occurred at H, started earlier and proceeded faster at H than at M. The very long interval between the earliest and last captures for *M. didyma* suggested the presence of several generations.

The POPAN model structures varied among species and in several cases, several equivalent models were selected (Table 2). Apparent survival ϕ s declined linearly or quadratically with time, typically with an effect of sex, except for some models for *M. didyma* (time-, or sex-constant), *M. athalia* M (constant sex-specific ϕ) and *M. cinxia* H (sex-independent ϕ). The capture probabilities p s responded factorially to time and sex in most cases, except for *M. athalia* H and *M. didyma* M (modelled as constant), and *M. britomartis* (daily p s equal for sexes). The proportional recruitments pent exhibited quadratic or cubic developments with time except for *M. didyma* H, in which it depended on sex only.

The estimated adult longevities ranged from 1.7 (*M. didyma* ♀♀ M) to 13.5 (*M. athalia* ♀♀ H) days, being 4–6 days for most systems. The total probabilities of captures p_{con} were mostly higher for $\sigma\sigma$, except for *M. didyma* H + M and *M. athalia* M (identical for sexes) and *M. aurelia* M (♀♀ more catchable).

In all species but *M. didyma*, the daily abundances N_t s followed domed curves typical for univoltine butterflies (Fig. 2). The total abundances N^t varied by two orders of magnitude. *M. cinxia* occurred in a few thousand at both sites. *M. aurelia* and *M. britomartis* (M only) formed abundant populations of $\approx 17,000$ and $\approx 20,000$ individuals, respectively. *M. athalia* was abundant ($\approx 11,000$) in M, while only a few hundred inhabited H. For *M. didyma* the demography parameters were estimated by rather simple model(s) for M, returning N^t of a few dozen individuals. For H, where a distinct summer peak occurred, modelling the entire flight period gave unrealistic estimates ($\approx 10^5$ individuals), while restricting the models to July returned a more realistic ≈ 700 individuals.

Wing wear analysis returned positive linear wear \sim day slopes regressions for all models except *M. athalia* ♀♀ H (with $n = 3$ captures only), and *M. didyma*, all models. Restricting *M. didyma* analysis to July captures returned significant regression, except for *M. didyma* ♀♀ M

Table 1

Summary of material obtained during mark-recapture campaign targeting five species of *Melitaea* checkerspots occurring on steppe grasslands of the Podyjí National Park.

Site / species	Sex	Dates	Marking days (duration)	Marked	Recaptured	%recaptured	Events
H							
<i>M. cinxia</i>	$\sigma\sigma$	16.v – 14.vi	27 (29)	800	122	15.3	947
	♀♀	16.v – 14.vi	28 (29)	371	39	10.5	416
<i>M. athalia</i>	$\sigma\sigma$	4.vi – 21.vi	9 (17)	63	8	12.7	71
	♀♀	9.vi – 21.vi	6 (13)	23	1	4.3	24
<i>M. didyma</i>	$\sigma\sigma$	24.v – 28.vii ^a	23 (65)	183	59	32.2	274
	♀♀	1.vi – 28.vii	13 (58)	60	17	28.3	79
M							
<i>M. cinxia</i>	$\sigma\sigma$	17.v – 19.vi	21 (33)	390	126	32.3	583
	♀♀	19.v – 18.vi	21 (30)	268	58	21.6	340
<i>M. athalia</i>	$\sigma\sigma$	28.v – 7.vii	31 (50)	1008	152	15.1	1188
	♀♀	1.vi – 17.vii	33 (47)	318	15	4.7	334
<i>M. didyma</i>	$\sigma\sigma$	23.v – 29.vii	14 (67)	28	10	35.7	41
	♀♀	28.v – 28.vii	6 (62)	12	2	16.7	14
<i>M. britomartis</i>	$\sigma\sigma$	10.vi – 22.vii	34 (42)	1572	182	11.6	1769
	♀♀	14.vi – 29.vii	34 (45)	707	69	9.8	783
<i>M. aurelia</i>	$\sigma\sigma$	12.vi – 22.vii	35 (40)	1721	228	13.3	1973
	♀♀	14.vi – 29.vii	34 (45)	1011	138	13.6	1175

^a likely multiple generations, one in May (23.v–5.vi), one in June–July (27.vi–17.viii).

Table 2
Results of modelling adult demography parameters of five Melitaeini checkerspots on xeric grasslands sites in the Podýjí National Park.

Site species	Selected models	AIC	ΔAIC	par	$N^{\sigma\sigma} \pm SE$	$N^{\sigma\sigma} \pm SE$	$N^{\sigma\sigma} \pm SE$	$\phi_{cont}^{\sigma\sigma} \pm SE$	$\phi_{cont}^{\sigma\sigma} \pm SE$	$\phi_{cont}^{\sigma\sigma} \pm SE$	$DD^{\sigma\sigma}$	$DD^{\sigma\sigma}$	$P_{em}^{\sigma\sigma} \pm SE$	$P_{em}^{\sigma\sigma} \pm SE$	$P_{em}^{\sigma\sigma} \pm SE$	$ww^{\sigma\sigma}$
H <i>M. cinxia</i>	$\varphi(T^{\sigma}) p(g + t) pent(g + T^{\sigma}) N(g)$	1977.3	0	28	3517 ± 355.4	2207 ± 286.2	0.81 ± 0.020	0.85 ± 0.030	4.7	6.2	0.07 ± 0.008	0.04 ± 0.008	0.081	0.073		
	$\varphi(g + T) p(C) pent(T^{\sigma}) N(g)$	1977.8	0.450	29	3546 ± 331.9	2288 ± 318.0	0.86 ± 0.088	0.93 ± 0.095	6.7	13.5	0.11 ± 0.064	0.04 ± 0.041	0.093	n.s.		
	$\varphi(g^{\sigma}T) p(C) pent(T^{\sigma}) N(g)$	154.4	0	9	317 ± 106.5	110 ± 40.7										
	$\varphi(g + T^{\sigma}) p(C) pent(g + T^{\sigma}) N(g)$	154.9	0.551	10	287 ± 103.1	116 ± 54.6										
	$\varphi(C) p(t) pent(g + T) N(g)$	156.3	1.898	10	318 ± 107.1	108 ± 40.1	0.90 ± 0.017	0.86 ± 0.041	9.5	6.6	0.15 ± 0.020	0.12 ± 0.029	0.011 (0.067) ^b	n.s. (0.034) ^b		
<i>M. didyma</i> ^a	$\varphi(C) p(t) pent(g + T) N(g)$	902.3	0.845	23	585 ± 100.2	154 ± 21.8										
	$\varphi(g) p(t) pent(g) N(g)$	902.4	0.902	23	565 ± 104.6	164 ± 27.4										
M <i>M. cinxia</i>	$\varphi(g + T) p(g + t) pent(g^{\sigma}T^{\sigma}) N(g)$	2177.9	0	36	1524 ± 390.8	1141 ± 212.2	0.78 ± 0.015	0.72 ± 0.029	4.0	3.0	0.18 ± 0.015	0.11 ± 0.019	0.126	0.080		
	$\varphi(g + T^{\sigma}) p(g + t) pent(g^{\sigma}T^{\sigma}) N(g)$	2178.8	0.913	33	1453 ± 338.1	1179 ± 227.3										
	$\varphi(g) p(g + t) pent(g^{\sigma}T^{\sigma}) N(g)$	2165.3	0	50	4905 ± 384.5	5341 ± 1482.4	0.84 ± 0.020	0.67 ± 0.006	5.9	2.5	0.03 ± 0.002	0.03 ± 0.002	0.077	0.072		
	$\varphi(g) p(C) pent(g + T^{\sigma}) N(g)$	179.3	0.000	9	49 ± 10.7	26 ± 9.1	0.84 ± 0.060	0.57 ± 0.196	5.7	1.7	0.34 ± 0.111	0.42 ± 0.361	-0.020 (0.061) ^b	n.s.(n.s.) ^b		
	$\varphi(C) p(C) pent(g + T^{\sigma}) N(g)$	180	0.71	10	51 ± 13.3	28 ± 10.1										
<i>M. britomartis</i>	$\varphi(C) p(C) pent(g + T^{\sigma}) N(g)$	180	0.724	9	54 ± 12.5	23 ± 6.6										
	$\varphi(g^{\sigma}T^{\sigma}) p(t) pent(g^{\sigma}T^{\sigma}) N(g)$	3120.7	0	53	12617 ± 1095.2	7349 ± 902.5	0.78 ± 0.013	0.80 ± 0.021	4.0	4.5	0.04 ± 0.004	0.03 ± 0.006	0.074	0.037		
<i>M. aurelia</i>	$\varphi(g + T) p(g + t) pent(g^{\sigma}T^{\sigma}) N(g)$	4425.5	0	49	10454 ± 6713	6551 ± 594.0	0.78 ± 0.001	0.77 ± 0.020	4.2	3.8	0.04 ± 0.004	0.06 ± 0.007	0.051	0.037		

Key: AIC – Akaike information criterion; ΔAIC – difference from the best-fitting model; par – number of models parameters; $N^{\sigma\sigma}/Q^{\sigma}$ – estimated total population size ($\pm SE$); $\phi_{cont}^{\sigma\sigma}/Q^{\sigma}$ – residence values returned from models with constant residence; $DD^{\sigma\sigma}/Q^{\sigma}$ – mean individual longevity (in days), obtained from constant residence models; $P_{em}^{\sigma\sigma}/Q^{\sigma}$ – probability of capture, returned from models with constant capture probability; $ww^{\sigma\sigma}/Q^{\sigma}$ – slopes of regressing wing wear of daily capture against serial number of marking day.

^a Modelling restricted to the distinct summer generation.

^b Results in brackets refer to July captures, i.e. presumed summer generation.

Table 3
Basic movement parameters of the five *Melitaea* butterflies co-occurring at Podyjí National Park xeric grasslands.

SITE / species	Total flight distance (TFD)			Mean single move (MSM)			Longest single move (LSM)			
	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	
H										
<i>M. cinxia</i>	♂♂	388 ± 455.7	212	2.1–2667.4	275 ± 269.0	202	2.1–1289.6	249 ± 248.7	173	2.1–1289.6
	♀♀	255 ± 405.4	156	5.0–2170.1	175 ± 169.4	133	5.0–743.7	160 ± 148.1	130	5.0–743.7
<i>M. athalia</i>	♂♂	304 ± 384.1	207	4.3–1366.9	215 ± 205.7	201	4.3–654.4	197 ± 172.4	191	4.3–469.3
	♀♀	42 ± 0.00 ⁹⁾	42	42.5–42.5	42 ± 0.00 ⁹⁾	42	42.5–42.5	42 ± 0.00 ⁹⁾	42	42.5–42.5
<i>M. didyma</i>	♂♂	528 ± 593.4	257	0.7–2280.6	289 ± 286.4	160	0.7–1023.3	238 ± 245.3	127	0.7–1023.3
	♀♀	216 ± 130.3	205	14.7–540.6	198 ± 132.7	201	14.7–540.6	195 ± 136.1	201	14.7–540.6
M										
<i>M. cinxia</i>	♂♂	494 ± 766.3	224	1.3–6133.4	250 ± 264.2	182	1.3–1376.1	213 ± 240.5	140	1.3–1376.1
	♀♀	258 ± 298.5	134	1.4–1117.4	173 ± 217.3	112	1.4–1117.4	158 ± 214.2	84	1.4–1117.4
<i>M. athalia</i>	♂♂	415 ± 570.1	213	0.5–4755.3	302 ± 303.6	189	0.5–1296.2	276 ± 271.1	174	0.5–1279.1
	♀♀	227 ± 351.3	116	0.4–1535.5	184 ± 194.0	116	0.4–762.7	170 ± 155.1	116	0.4–511.8
<i>M. didyma</i>	♂♂	185 ± 252.4	102	27.4–885.0	164 ± 256.0	62	27.4–885.0	160 ± 257.8	54	27.4–885.0
	♀♀	54 ± 27.4	54	34.3–73.1	54 ± 27.4	54	34.3–73.1	54 ± 27.4	54	34.3–73.1
<i>M. aurelia</i>	♂♂	218 ± 289.7	101	0.1–2008.8	182 ± 216.1	93	0.1–981.1	173 ± 208.7	92	0.1–933.8
	♀♀	172 ± 289.8	74	2.6–1630.4	127 ± 170.2	71	2.6–957.9	115 ± 147.9	65	2.6–957.9
<i>M. britomartis</i>	♂♂	264 ± 310.8	133	0.4–2038	213 ± 222.8	120	0.4–1181.5	201 ± 213.7	113	0.4–1181.5
	♀♀	176 ± 209.6	101	0.9–1184.9	152 ± 151.8	97	0.9–696.3	145 ± 147.4	83	0.9–696.3

($n = 12$). The fitted regressions slopes differed among species and sexes (all data: $F(16, 10372) = 212.7, P < 0.0001$; after pruning *M. didyma* data: $F(16, 10341) = 225.9, P < 0.0001$), their comparison revealed steeper wing wear increases in ♂♂ of all species and a steeper increase in *M. cinxia*♂♂ M than *M. cinxia*♂♂ H (Supplementary material II).

3.2. Adult mobility

The maximum total flight distance for all species except those recaptured in low numbers (*M. athalia*♀♀ H, *M. didyma*♀♀ H and *M. didyma*♂♂ + ♀♀ M) exceeded 1 km, being > 5 km for *M. cinxia*♂♂ M, > 4 km for *M. athalia*♂♂ M, and > 2 km for *M. cinxia*♂♂ + ♀♀ H, *M. didyma*♂♂ H, *M. aurelia*♂♂ and *M. britomartis*♂♂. The longest single moves and maximum single moves were a few hundred metres, again except for systems with very few recaptures, and exceeded 1 km for six systems (Table 3).

Comparing the movement parameters using generalised linear models (Supplementary material III) revealed that values of the parameters were positively influenced by times between captures H_r , numbers of recaptures C , or a combination of these covariates. In addition, ♂♂ were more mobile than ♀♀ in all species but *M. didyma*, in which the sexes did not differ. In the three species inhabiting two sites, movement parameters were identical, except for maximum single move of *M. cinxia*, longer in H. *M. athalia* was the most mobile species, followed by *M. cinxia*, *M. didyma*, *M. britomartis* and *M. aurelia*.

Fitting Inverse power functions (Supplementary material IV) corroborated these results. The functions differed in their slopes for sexes treated separately ($F(9, 1432) = 110.8, P < 0.0001$), but not for sexes combined ($F(4, 1413) = 0.71, df = 4, P = 0.448$). Post-hoc comparison of function slopes showed that ♀♀ were more mobile than ♂♂ in *M. athalia* and *M. britomartis*; the sexes did not differ in *M. didyma*; and ♂♂ were more mobile in the remaining species. *M. athalia*♀♀ were more mobile than all the other systems, and *M. aurelia*♂♂ were more mobile than all systems, except *M. athalia*♂♂ + ♀♀. *M. aurelia*♀♀ were the least mobile of all systems.

3.3. Adult habitats

Both land uses and land covers explained the distribution of adults highly significantly at both buffer levels, with explained variations 3–4%. The percentages decreased in covariate models, implying that both categories or predictors affected the distribution of adults (Table 4).

For covariates-controlled land uses, the 20 m diameter achieved the best fit (Fig. 3). The first ordination axis separated *M. aurelia* and *M. britomartis* (neglected, earth walls) from *M. cinxia* and *M. didyma* (mown or sheep grazed), with *M. athalia* in an intermediate position. *M. aurelia* preferred earth walls within mown grasslands, *M. britomartis* preferred neglected locations. *M. didyma* and *M. cinxia* showed an association with sheep grazing, *M. athalia* with forest. For covariates-controlled land covers, the 50 m diameter model explained most variation; it separated *M. athalia* and *M. britomartis*, both associated with trees or shrubs, from *M. cinxia* and *M. didyma*, associated with grassy surfaces, with *M. aurelia* in an intermediate position. *M. aurelia* avoided trees and scrub, *M. cinxia* displayed affinity to barren patches with exposed rock, and *M. didyma* preferred medium-sward grasslands and rocks.

3.4. Larval nests

We failed to detect larval nests in H but detected the following number of occupied 5 m-radius plots/ nests in M: *M. aurelia* 13/ 52; *M. britomartis* 5/ 12; and, *M. cinxia* 2/ 2. In one instance, *M. britomartis* co-occurred with *M. cinxia* within a plot. The mean(± SD)/ median/ range of nests per occupied plot were 4(± 5.1)/ 2/ 1–20 (*M. aurelia*), and 2(± 1.4)/ 2/ 1–4 (*M. britomartis*). All *M. aurelia* nests were on *Plantago media*. *M. britomartis* used *V. spicata* ($n = 5$) and *V. teucrium* ($n = 8$). The two *M. cinxia* nests were on *V. spicata* ($n = 1$) and *V. teucrium* ($n = 1$).

M. aurelia nests were placed at lower heights on the host plant (Mean ± SD = 4 ± 4.2 cm), in short sward (16 ± 11.7 cm), surrounded by some barren ground (10 ± 10.2%). *M. britomartis* nests were at a greater height (23 ± 7.0 cm), within taller sward (29 ± 9.8 cm) and minimum bare ground (3 ± 5.5%) (details: Supplementary material V).

Covers of host plants were the best predictor of the nests' presence. Disregarding this effect, we obtained a marginally significant model associating *M. aurelia* (and its host plant) with ditches and slopes, and *M. britomartis* (and its host plants) with short (1–2 m) shrubs (Fig. 4).

3.5. Wider landscape occupancy

Out of the eight additional steppe patches surveyed, we found *M. cinxia* at three and *M. britomartis* together with *M. aurelia* at one (Fig. 1).

Table 4

Effects of land covers and land uses on the distribution of capture events, carried out at two buffers around each capture point, in both cases first separately for covers and uses, and after setting one of the groups of predictors as covariable (i.e., ~predictor | covariable). Covariate models explaining higher percentage of variation are in **bold**. Key: **Ax1–Ax4**: eigenvalues of canonical axes. **var**: percentage variation explained by the model. ***: $P < 0.001$.

Buffer / model	Ax1	Ax2	Ax3	Ax4	var	F, P (ax1)	F, P (all axes)
20 m							
Land covers	0.0255	0.0080	0.0007	0.0004	3.4%	268.0***	91.6***
Land uses	0.0237	0.0074	0.0022	0.0009	3.4%	248.0***	90.6***
Covers uses	0.0146	0.0022	0.0004	0.0001	2.8%	250.0***	74.7***
Uses covers	0.0164	0.0042	0.0015	0.0002	3.7%	243.0***	83.4***
50 m							
Land covers	0.0309	0.0114	0.0019	0.0001	4.4%	326.0***	119.1***
Land uses	0.0211	0.0086	0.0025	0.0009	3.3%	221.0***	87.5***
Covers uses	0.0149	0.0030	0.0002	0.0001	3.4%	295.0***	90.7***
Uses covers	0.0114	0.0038	0.0011	0.0002	2.6%	185.0***	68.0***

4. Discussion

The coexistence of five checkerspot butterflies on xeric grasslands of the Podyjí National Park is facilitated by differences in resource and habitat use, which correspond with their phenology, population structure and mobility. For practical conservation, perhaps the most interesting finding was the absence of *M. britomartis* from site H, a past CZ stronghold of the species, indicating a recent loss, and the huge populations of *M. aurelia* and *M. britomartis* at site M, which is presently crucial for their conservation within the National Park.

4.1. Adult demography

Population size is indisputably a decisive factor for conserving animal populations. In this respect, the adult numbers of *M. cinxia* (lower thousands at both sites), *M. athalia*, *M. aurelia*, *M. britomartis* (all in higher thousands at site M) indicated abundant self-containing populations, potentially able to withstand even the remarkable abundance size fluctuations described for related species (e.g., [McLaughlin, Hellmann, Boggs, & Ehrlich, 2002](#); [Vrabec, Bubova, Kulma, Krasa, & Nowicki, 2019](#)). Abundances of *M. athalia* at H, and *M. didyma* at both sites, in contrast, indicated either extremely small populations, or, more

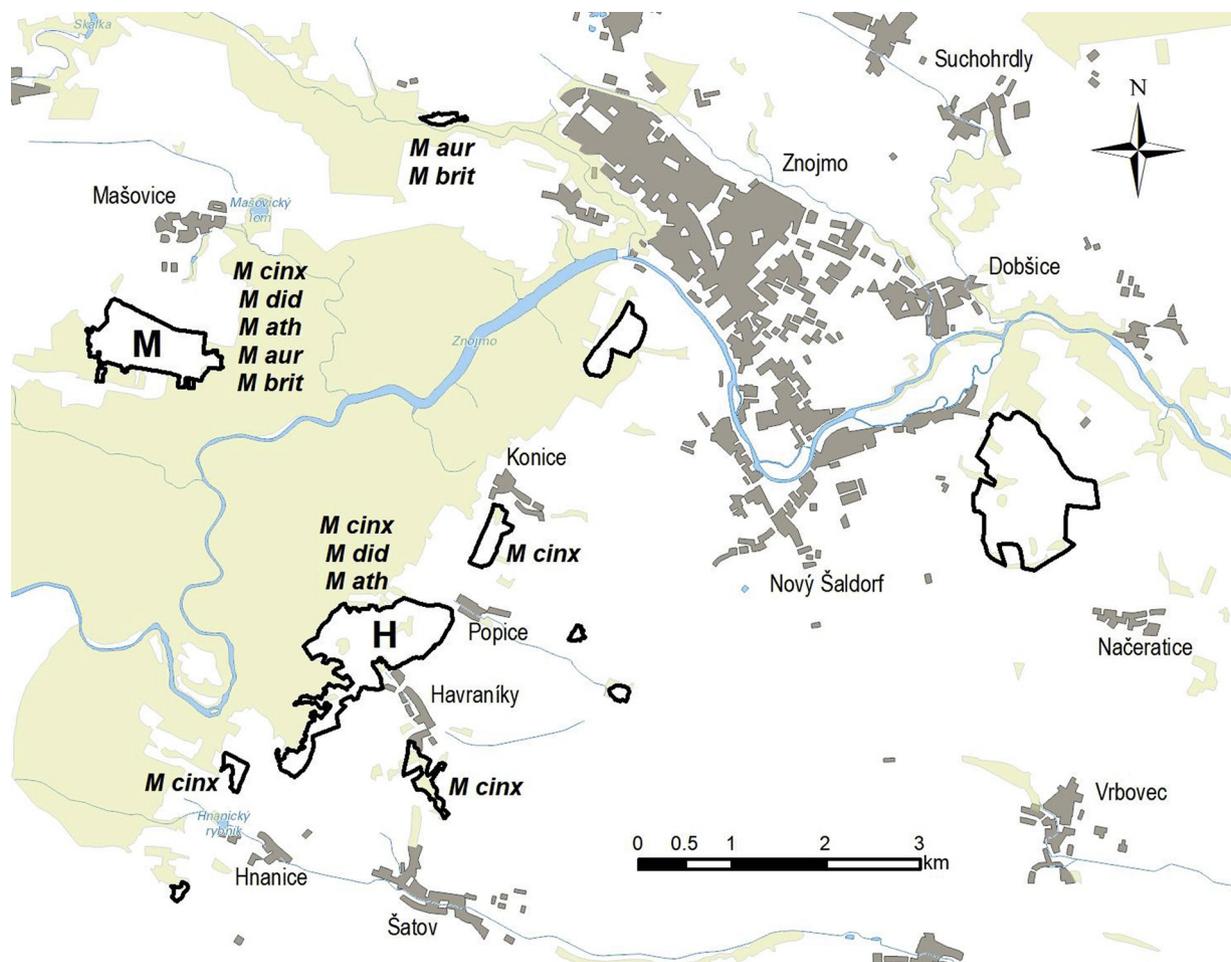


Fig. 1. Map of the study area showing the forested Dyje river canyon, the large xeric grassland patches H and M at canyon rims, and other xeric grassland patches amidst farmed landscape, with Melitaeini checkerspot records indicated separately for each grassland patch. Dark grey – built up land, light grey – forest, white – grasslands or arable land.

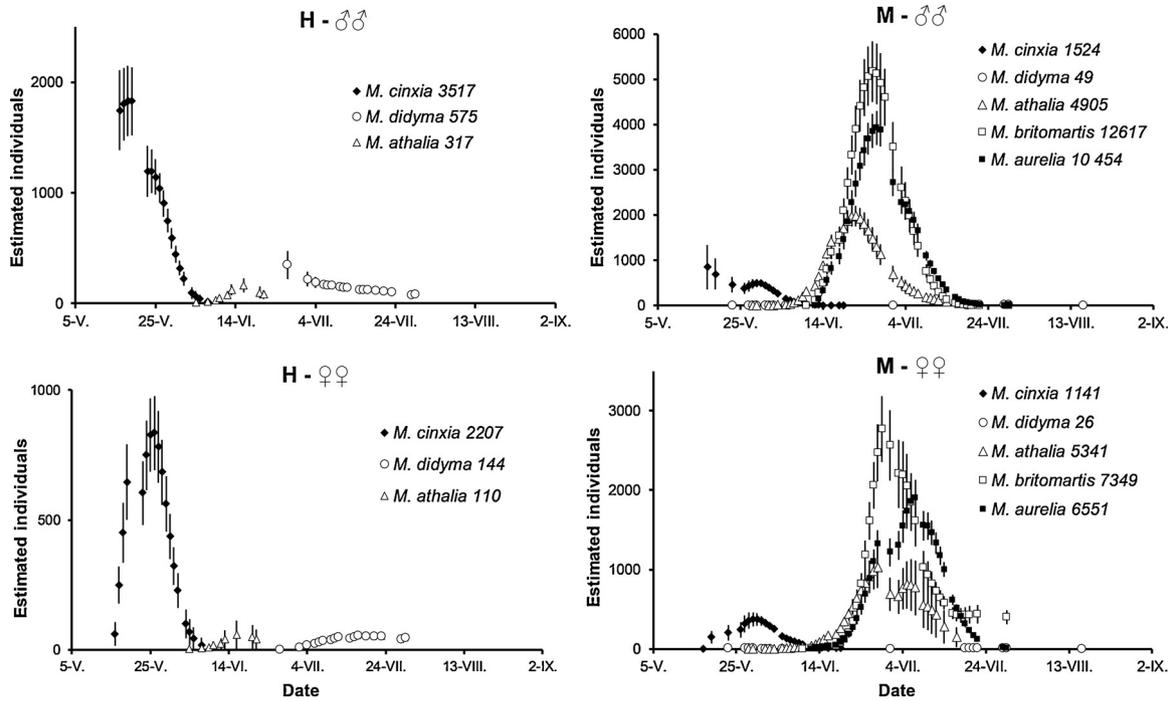


Fig. 2. Estimates of daily adult population sizes ($N_{is} \pm SE$) for the five species of checkerspot butterflies occurring at two patches of xeric grasslands, H and M, of Podyjí National Park.

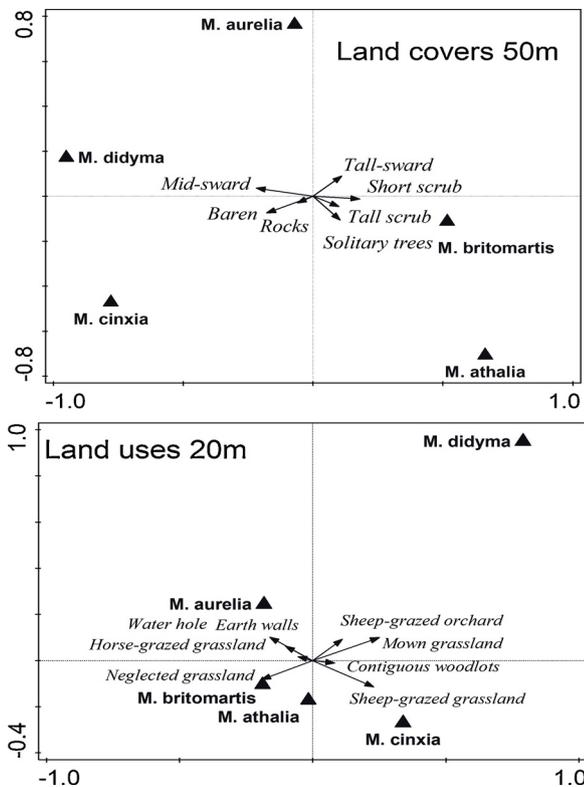


Fig. 3. RDA ordination biplots showing the effects of land covers (top) and land uses (bottom) on distribution of adult captures of five species of checkerspot butterflies, occurring at xeric grasslands of Podyjí National Park. The illustrated models explained higher variation from two alternatives based on 20 m and 50 m diameter buffers around capture points and tested for partial effect of land covers / uses after setting land uses / covers as covariables.

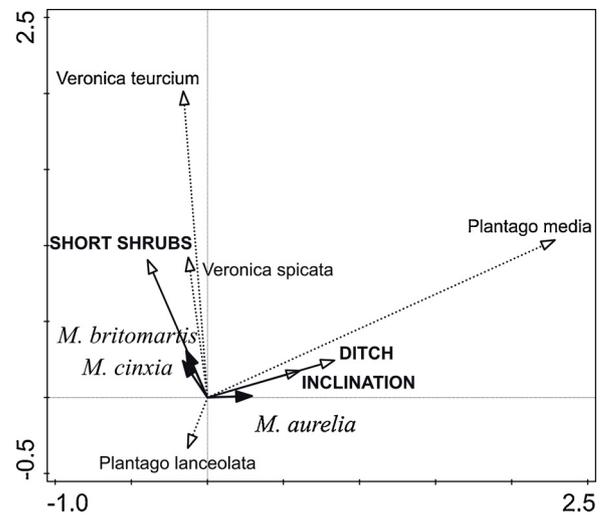


Fig. 4. RDA ordination triplot showing the factors influencing the larval nest presence. Spatial position of plots (x^2 polynomial, adjusted explained variation 2.5%, eigenvalue = 0.031, $F = 4.6$, $P = 0.001$) was set as covariate, covers of host plants (the best explanatory variable, adjusted explained variation = 52.4%, canonical eigenvalues = 0.497, 0.022, 0.000, 1st axis $F/P = 146.0/0.001$, all axes $F/P = 40.1/0.001$) was depicted as a supplementary variable. The resulting model's parameters were: adjusted explained variation = 6.9%, canonical eigenvalues = 0.082, 0.004, 0.000, 1st axis $F/P = 12.9/0.07$, all axes $F/P = 4.5/0.07$.

likely, interconnection with other colonies not covered by our study. The phenologically earliest species, *M. cinxia*, peaked at site H a few days prior to site M, despite just 3 km aerial distance between the sites. The earlier phenology at H was supported by a steeper wing wear regression line. It probably reflected the warmer character of H (south-exposed, lower-elevated). Phenology shifts among closely situated butterfly colonies are common (Bennett, Betts, & Smith, 2014; Weiss, Murphy, & White, 1988; Zimmermann, Blazkova et al., 2011). By desynchronising within-patch dynamics, they contribute to

metapopulation persistence on landscape scales. An earlier phenology at H also applied to *M. athalia*♂♂.

Flight patterns of the least abundant *M. didyma* differed between the sites. At M, the adults were present already in May, occurred without a clear peak until late July, and we encountered a few individuals during the larval nest survey in late August. In H, a few worn May individuals were followed by a gap in occurrence, and then a distinct July peak. Wing wear analysis suggested that we marked the tail of an early spring generation, which was followed by a distinct July generation in H and by indistinct occasional occurrence at M. In this species, voltinism increases clinally towards the South (Macek et al., 2015; Tolman & Lewington, 2008). *M. didyma* is currently re-expanding northwardly in Central Europe, concurrently with increasing generation numbers. The butterfly was first seen at site M a decade ago, in contrast to H, where it had occurred continuously (cf. Cizek et al., 2013; Slancarova et al., 2014). Possibly, we observed a spearhead of the re-expansion, with resident butterflies and their progeny intermixing with individuals arriving from elsewhere in M, thus blurring distinct generations.

4.2. Mobility and landscape occupancy

The maximum distances crossed by most of the species x sex combinations imply that within H and M sites, the checkerspot form interconnected population units. The movement parameters were similar to values published for identical or related species (e.g., Casacci et al., 2015; Fric, Hula, Klimova, Zimmermann, & Konvicka, 2010; Hanski, Kuussaari, & Nieminen, 1994; Novotny et al., 2012; Wahlberg et al., 2002; Warren, 1987a; Zimmermann, Fric et al., 2011). We did not detect movements between H and M sites, despite the rather short direct distance separating them (Fig. 1), rather long distances crossed by *M. cinxia* and *M. athalia* individuals within the sites (Table 3), and interpatch movements of similar or even higher lengths detected for other Melitaeini (e.g., Hanski et al., 1994; Zimmermann, Fric et al., 2011). Our interpretation, besides the rather low chance to capture rare immigrants arriving into abundant populations, is that dispersing individuals follow permeable landscape structures while avoiding inhospitable ones (Dover & Settele, 2009; Ricketts, 2001; Schmitt, Varga, & Seitz, 2000). The forested river canyon with minimum open spaces (Miklin, Miklinova, & Cizek, 2016) and the abrupt forest-farmland transition along its perimeter likely act as dispersal barrier for grassland specialists. Flying from M to H around the perimeter would require crossing much longer distance across intensively-used landscape, including an urban area, than a direct flyover (cf. Fig. 1).

While the descriptive movement parameters pointed to a higher male mobility in all species except *M. didyma*, a more complex situation appeared from IPF models, which calculate with probability densities rather than mere averages. The models suggested higher female than male mobility for *M. athalia*, and equal mobility of sexes for *M. didyma*. Female mobility is decisive for establishing new colonies (Hanski, 1999; Zimmermann, Fric et al., 2011). In Melitaeini, with their habit of laying large egg clutches, fresh females carrying heavy egg loads disperse less than older ones (Saastamoinen, 2007). This further diminishes chances to detect dispersers (Duploux, Ikonen, & Hanski, 2013). Notably, the two species with relatively high female mobility lay smaller egg clutches, and thus carry lower weights, than the remaining three species.

Both basic movement parameters and IPFs revealed identical mobility hierarchy, with the more widely distributed *M. athalia* and *M. cinxia* being more mobile than the regionally rare *M. britomartis* and *M. aurelia*. This conforms with a positive mobility-distribution relationship, repeatedly observed for butterflies (e.g., Cowley et al., 2001; Bartonova, Benes, & Konvicka, 2014; Slancarova et al., 2015). The intermediate position of *M. didyma* may be linked to its ongoing re-expansion. *M. cinxia* is currently also recolonising parts of the Czech Republic and displays a good recolonisation capacity in Finland (Hanski et al., 2017). The least mobile *M. aurelia*, on the other hand, failed to colonise H from M during an entire decade.

The survey of steppe patches in the wider environs (Fig. 1) suggested that landscape-scale coexistence patterns cannot be predicted from within-sites situations. We did not detect any of the butterflies in any of the steppe patches amidst arable fields easterly from the town of Znojmo, but *M. aurelia* and *M. britomartis* inhabited a steppe islet 3.5 km northeasterly from M. Presumably, insufficient resources and poor habitat quality (approximate by patch size: Ojanen et al., 2013) exclude the butterflies from very small patches, whereas contiguous woodland, huge arable units (cf. Salek et al., 2018) or urbanised areas restrict dispersal among the relatively large patches.

4.3. Habitat requirements

Studying butterfly habitat use by relating positions of captures to pre-defined land use and cover categories risks biases due to *a priori* delimitation of the categories. A more legitimate approach would relate activity patterns of the animals to their vital resources (e.g., Maes et al., 2014; Tropek, Cizek, Kadlec, & Klecka, 2017). However, the high density of the studied populations precluded recording detailed circumstances of each capture. Still, the five species differed in their responses to the predictors used, and the resulting patterns agreed both with background life history knowledge and the information obtained on their larval habitats.

As in other studies, *M. athalia* inclined towards woodland edges, trees and tall shrubs (Hodgson, Moilanen, Bourn, Bulman, & Thomas, 2009; Warren, 1987b); it also readily colonises experimental woodland openings within the forested Dyje canyon (Sebek et al., 2015). The much lower numbers detected at the prevailing steppe site H compared to the more scrubby site M, as well as the relatively high mobility, allow to conjecture that at H, our marking captured only a part of a (meta)population inhabiting the canyon's woodlands. Site M, partly covered by tall shrubs and sparse woodlots, currently offers the species optimal conditions.

For *M. aurelia*, the land cover and land use analyses described the preferences using different, but biologically equivalent, variables. The former pointed to short grasslands, whereas the latter revealed an association with earth walls and ditches, where the larval nests also occurred. In Germany, the species reportedly requires high density of the *Plantago media* host plant, combined with abundant nectar (Eichel & Fartmann, 2008). At M, *P. media* grows abundantly both at the mesophilous grasslands on flat surfaces, which were machine-mown or sheep-grazed in the year of the study, and along the sparsely vegetated ditches. Adults, however, avoided the flat surfaces, which lacked nectar during their flight. Depending on timing, machine mowing may damage egg batches or larval nests (Konvicka, Hula, & Fric, 2003; van Noordwijk et al., 2012). Possibly, the scarcity of nectar at freshly mown sections, combined with nectar abundance along the ditches, provides the butterflies a safe oviposition clue.

M. britomartis adults were associated with neglected and tall (0.75–1.5 m) vegetation, in which grasses and forbs mixed with short shrubs and which contained abundant *Veronica spicata* and *V. teucrium* host plants. Very few habitat descriptions exist for this species, except for an Italian population from a humid biotope (Cerrato et al., 2014). Still, the few mentions in literature (e.g., Klimczuk, 2011), and observation from more easterly parts of its range (i.e., Southern Urals, J. Beneš, personal communication) agree that *M. britomartis* inhabits sparse woodlands or overgrown pastures. Historically, it occurred also within the canyon's forests (Sumpich, 2011), which used to be much sparser than at present owing to coppicing and grazing (Miklin et al., 2016). Having rather restricted mobility, *M. britomartis* has not yet colonised experimental woodland openings within the canyon (Sebek et al., 2015).

In line with a preference for pastures with low-intensity use (Hanski et al., 2017; Ojanen et al., 2013; Zhou et al., 2012), *M. cinxia* utilised short-sward grasslands near woodland edges, typically grazed by sheep. Such sites contained rich growths of *Plantago lanceolata*, the host plant

most frequently reported in literature, and we observed egg-laying there during the marking. However, we failed to locate larval nests there, and found just two nests within neglected tall sward. The 2017 season was extremely hot and dry, which can be detrimental for *M. cinxia* host plants and larvae (Curtis & Isaac, 2015; Tack, Mononem, & Hanski, 2015). The species, however, was present at both sites again in the following year, when we found solitary spring larvae feeding on *P. lanceolata*. Further work is required to ascertain details of *M. cinxia* larval biology in the area.

M. didyma preferred medium-sward grasslands managed by grazing or mowing, plus exposed rocks. Klimova (2007) described its preference for short, sun-scorched swards, and development on extremely xerophilous *Linaria genistifolia*, in a nature reserve 35 km to the North. *L. genistifolia* grows abundantly at exposed rocks in SW parts of site H, but literature lists a wider host plant spectrum for this species (Macek et al., 2015). We found a single larva feeding on the congeneric but more mesophilous *L. vulgaris* in late August 2017. *M. didyma* is considered an extremely warm-requiring species in C Europe, but its requirements are relaxed towards southern parts of its range. It displays unusually high cytochromoxidase I variation (Pazhenkova & Lukhtanov, 2016) and this cryptic diversity might be related to sometimes conflicting reports regarding its ecology (cf. Dinca, Lukhtanov, Talavera, & Vila, 2011; Junker et al., 2015).

4.4. Prospects of feral horses grazing

Despite spatial overlaps and syntopic distribution (cf. Batori et al., 2012), the coexistence of three (H) and five (M) checkerspot species at the studied grasslands is facilitated by differences in habitat use. Their requirements follow a gradient from tall scrub and woodland edges (*M. athalia*), through neglected scrubby grasslands (*M. britomartis*), short-sward but closed turf grasslands (*M. cinxia*) to open-turf patches (*M. aurelia*). *M. didyma* may be changing its requirements at present, similarly to other butterflies benefitting from warming climate (Davies, Wilson, Coles, & Thomas, 2006; O'Connor, Hails, & Thomas, 2014). This gradient is reflected by mobility patterns, with woodland *M. athalia* being the most mobile, and open-turf *M. aurelia* the least mobile. Local population sizes presumably reflect local supply or the species' vital resources, whereas the current distribution is linked to management history of the sites.

The rural commons forming site H went through a phase of neglect in the post-war decades. An analysis of aerial photographs (Miklin et al., 2016) showed that the transition from grasslands to closed woodlands was historically formed by a wide belt of wooded meadows and scrub. During the neglect phase, some species requiring large areas of open-turf grasslands were lost (e.g., *Chazara briseis*: Kadlec, Vrba, & Konvička, 2009; Sumpich, 2011), whereas those of neglected grasslands and scrub, including *M. britomartis*, benefitted. Subsequent establishment of conservation mowing, scrub removal and sheep grazing were applied to the "steppic" sections of the locality but not to the adjoining "forested" parts. This disadvantaged the later-succession species.

Past military use created the outstanding diversity of conditions at site M (Cizek et al., 2013; Reif, Marhoul, Cizek, & Konvicka, 2011), including the structures preferred by *M. aurelia*. An increase of shrubs and tall-sward patches following cessation of military use created optimal conditions for *M. britomartis*. Its population is by far the largest in the country, and the last remaining in the National Park.

Speculating on the future effects of grazing by Exmoor ponies, consider that entire areas of the localities are within the dispersal capacity of all the species studied. Hence, a localised alteration of conditions should not have a detrimental effect, provided that suitable conditions will arise in proximity (Hodgson et al., 2009). By maintaining or expanding the short-sward conditions without the negative effects of mowing, the ponies should positively affect *M. aurelia*, *M. cinxia* and *M. didyma*. Contrary to sheep, horses prefer grasses over forbs, and contrary to machine mowers, the disturbance is gradual,

rather than abrupt. Regarding *M. athalia*, the horses will likely halt the expansion of the tall shrubs at M by winter browsing on young twigs and fruits but will unlikely suppress larger shrubby growths. The effect on the butterfly will then be neutral.

A conflict may arise with the priority species *M. britomartis*, because the horses may suppress the tall-sward patches crucial for the butterfly. Therefore, grazing pressure on the vegetation and associated butterflies should be closely monitored, and stocking by horses flexibly regulated to ensure the tall grass patches presence. Other options include establishment of temporarily shifting grazing refuges (Smit, Ruifrok, van Klink, & Olff, 2015; van Klink & WallisDeVries, 2018), or gradual expansion of the grazed area towards the adjacent forests, perhaps after opening the currently closed canopy by selective trees removal (Sebek et al., 2015). Expansion of grazing towards the forests at H should be accompanied by assisted recolonisation by *M. britomartis* stock from M.

The biota of European grasslands had evolved side-by-side with native megafauna, which maintained a dynamic grasslands-forest mosaics (Galetti et al., 2018; Johnson, 2009). Specialised invertebrates tracked suitable conditions via metapopulation processes. Following the demise of native ecosystem engineers, pre-industrial agriculture maintained the shifting biotope mosaics. This abruptly changed with agricultural (and forestry) intensification, which caused defaunation on large scales (Dirzo et al., 2014). Refaunation of the best grassland sites by native megafauna is highly desirable, although contrary to the past, the large herbivores will operate within spatially restricted areas, increasing the risks of deleterious effects. Close monitoring of the effects, and flexible reactions by managers, shall ensure that refaunation actions will benefit, rather than harm, local biotic diversity.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jnc.2019.125755>.

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