DE TTK

1949

HABITAT USE AND POPULATION STRUCTURE OF PROTECTED BUTTERFLIES

VÉDETT NAPPALI LEPKÉK ÉLŐHELYHASZNÁLATA ÉS POPULÁCIÓSZERKEZETE

Egyetemi doktori (PhD) értekezés

ÖRVÖSSY NOÉMI

témavezető
DR. VARGA ZOLTÁN

DEBRECENI EGYETEM
Természettudományi Doktori Tanács
Juhász-Nagy Pál Doktori Iskola
Debrecen, 2014.

*Ezen értekezést a Debreceni Egyetem Természettudományi Doktori Tanács **Juhász-Nagy Pál** Doktori Iskola **Biodiverzitás** programja keretében készítettem a Debreceni Egyetem természettudományi doktori (PhD) fokozatának elnyerése céljából.*

Debrecen, 2014. december 10.

Örvössy Noémi

*Tanúsítom, hogy Örvössy Noémi doktorjelölt 2004- 2014 között a fent megnevezett Doktori Iskola **Biodiverzitás** programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.*

Debrecen, 2014. december 10.

Prof. Dr. Varga Zoltán

HABITAT USE AND POPULATION STRUCTURE OF PROTECTED BUTTERFLIES

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a biológia. tudományágban

Írta: Örvössy Noémi okleveles biológus

Készült a Debreceni Egyetem Juhász-Nagy Pál doktori iskolája
(Biodiverzitás programja) keretében

Témavezető: Dr. Varga Zoltán

A doktori szigorlati bizottság:
    elnök: Dr. Pócsi István   ....
    tagok: Dr. Rózsa Lajos   ....
                     Dr. Földvári Mihály   ....

A doktori szigorlat időpontja: 2013. február 13.

Az értekezés bírálói:
                     Dr. ....
                     Dr. ....
                     Dr. ....

A bírálóbizottság:
    elnök: Dr. ....
    tagok: Dr. ....
                     Dr. ....
                     Dr. ....
                     Dr. ....

Az értekezés védésének időpontja: 2015.

Table of content

INTRODUCTION

Biodiversity crisis and butterflies

Biodiversity is declining rapidly throughout the world, caused by human impacts. Therefore, halting the biodiversity decline requires immediate measures planned on solid scientific background. The current biodiversity crisis appears more critical among butterfly species than among other species (THOMAS 1991; THOMAS *et al.* 2004). The diversity of butterfly species has decreased to a great extent in Europe; some surveys show an even larger decrease than in bird or plant species (e.g. THOMAS *et al.* 2004; VAN STRIEN *et al.* 2009). Butterfly populations disappear more rapidly than bird or plant populations due to their short life span and lack of dormant propagules (THOMAS *et al.* 2004). However, HAMBLER *et al.* (2011) suggested that long-term extinction rates are similar among birds and butterflies, but that the latter react more rapidly to changes in habitat quality or climate. Populations of "specialist" species have declined more than those of "generalist" species (WARREN *et al.* 2001), putting them at even greater risk of extinction.

The Millennium Ecosystem Assessment (HASSAN *et al.* 2005) summarises the current biodiversity crisis and the decline of biodiversity in many taxa. Butterfly decline was identified in areas where detailed monitoring data are available. The overall European decline in distribution of butterflies is 11% over the last 25 years. The distributions of the 25 most generalist species are declining only slowly (-1%) compared to specialist species of grasslands (-19%), wetlands (-15%) and forests (-14%) (VAN

SWAAY *et al.* 2006). The best monitoring datasets are available from the Netherlands and UK. In the Netherlands (VAN SWAAY 1990), of the 63 species assessed, 29 decreased or became extinct. Distributions of British butterflies also have decreased by 71% over the past 20 years (THOMAS *et al.* 2004). The main reasons for butterfly diversity decline in Europe are habitat loss, habitat fragmentation and changes in land management (MAES & VAN DYCK 2001; PULLIN 2002; SKÓRKA *et al.* 2007; WARREN *et al.* 2001; HANSKI 2003; PARMESAN 2003).

Threatened butterfly habitats in agricultural landscapes

As European landscapes have long been dominated by humans, many species rich habitat types rely on the low-intensity agricultural use typical of earlier agronomic eras, which now require conservation-oriented habitat management to maintain them. Around 50% of butterfly species live in such semi-natural grasslands (ERHARDT & THOMAS 1991), where management is necessary to maintain their current populations (VAN SWAAY & WARREN 1999; VAN SWAAY 2002). Agricultural landscapes may be affected by either intensification or abandonment, both of which can diminish formerly suitable butterfly habitats (STRIJKER 2005).

Agricultural intensification is one of the major forces behind the current decline of rural landscape biodiversity, especially in Western Europe (DOVER *et al.* 2011; KLEIJN *et al.* 2009; MAES & VAN DYCK 2001). Management, generally in the form of grazing or mowing, maintains grasslands as a habitat. Intensive management decreases butterfly diversity, while extensive management maintains grassland habitat and enhances

diversity (KRUESS & TSCHARNTKE 2002). In Eastern regions, abandonment of grassland habitats is frequent, and a crucial question for butterfly conservation (SKÓRKA *et al.* 2007). Cessation of management can enhance short-term biodiversity and butterfly abundance, but later deteriorate the habitat (DOVER *et al.* 2011; SKÓRKA & LENDA 2010; VAN SWAAY 2013).

Intensive agriculture generates large and homogeneous landscape units around less intensively used grassland remnants and causes fragmentation (KÉRY *et al.* 2001; SHREEVE & DENNIS 2011; STOATE *et al.* 2009). The patchiness of semi-natural grassland habitats raises the question of how landscape configuration and composition affect butterfly diversity and abundance. The area effect is observable in fragmented grasslands in most studies (KRAUSS *et al.* 2003; STEFFAN-DEWENTER & TSCHARNTKE 2000), although others show no such effect (ÖCKINGER & SMITH 2006). Landscape heterogeneity generally increases diversity (WEIBULL & OSTMAN 2003; ÖCKINGER *et al.* 2012). When the effects of configurational and compositional landscape heterogeneity are separated, butterfly abundance increases with compositional heterogeneity, and butterfly diversity increases with configuration heterogeneity (SLANCAROVA *et al.* 2013).

Landscape homogenisation has a detrimental effect on butterfly community composition. Several endangered species still exist in heterogeneous landscapes (EKROOS *et al.* 2010; SLANCAROVA *et al.* 2013, and compositional heterogeneity is positively correlated with the diversity of generalist butterfly species, but has no effect on specialist species (KRAUSS *et al.* 2003; BERGMAN *et al.* 2004). Heterogeneous landscape configurations are best for species whose populations use multiple sites of

3

rarer biotope types within the landscapes, whereas heterogeneous configuration does not affect species persisting at isolated sites or those utilising common biotope types (DAPPORTO & DENNIS 2013; SLANCAROVA *et al.* 2013). FILZ *et al.* (2014) studied the combined effects of climate change, landscape configuration and habitat quality. Their conclusion was that habitat specialist species are at high risk of extinction. Conservation practices could enhance butterfly diversity by dividing large homogenous landscapes into separate elements, using stepping stones, hedges and herbaceous stripes (CROXTON *et al.* 2005; TSCHARNTKE *et al.* 2002; WALKER *et al.* 2006), in order to increase the amounts of resources within landscapes (SHREEVE & DENNIS 2011). Diversification of management also enhances butterfly population density (SAMWAYS *et al.* 2010; CIZEK *et al.* 2012).

Fragmentation and change in land management seriously threaten wet meadows (HALADA *et al.* 2011), which are among the most important and endangered habitats of butterflies in Europe (KÜHN *et al.* 2005). More than half of the Hungarian Prime Butterfly Areas is wet meadows (VAN SWAAY & WARREN 2003). It is now widely demonstrated that agricultural intensification reduces the diversity and abundance of butterflies associated with extensively managed wet meadows (e.g. VAN SWAAY & WARREN 1999; KONVIČKA *et al.* 2003; ZIMMERMANN *et al.* 2005). Habitat degradation and fragmentation of wet meadows have caused the decline of several butterfly species, including *Coenonympha oedippus* and *Maculinea teleius* (VAN SWAAY & WARREN 1999; NOWICKI *et al.* 2007; SKÓRKA *et al.* 2007; VAN SWAAY *et al.* 2010a).

Population structure and conservation status of protected butterflies

While a complete description of biodiversity on a large scale is impossible, it is feasible to monitor changes in biodiversity using certain indicator species. Groups of species that are easy to monitor or have a special importance in the ecosystem services throughout an extensive network of sites are good indicators and can be a basis of monitoring (PEREIRA *et al.* 2013). Butterflies are adequate indicators of change for many terrestrial insect groups (THOMAS 2005). The presence, absence or abundance of an indicator species reflects a specific environmental condition. Presence of and changes in populations of indicator species mirror those of other species in the community (SIMBERLOFF 1998; FLEISHMAN *et al.* 2000). Butterfly Monitoring Schemes provide data for evaluating changes in biodiversity (VAN SWAAY *et al.* 2008).

For more effective habitat conservation, the "umbrella species" concept was developed. Umbrella species are equally or even more sensitive to environmental changes than the other species present in the habitat. They are chosen by conservationists based on their ability to represent changes occurring in the most taxa possible in an area. In the case of butterflies, FLEISHMAN *et al.* (2000) applied this definition: "species whose conservation confers a protective umbrella to numerous co-occurring species". *Maculinea* species can be considered as indicators and umbrella species on hay meadows, due to their special life cycle and sensitivity to environmental changes (THOMAS *et al.* 2005, SKÓRKA *et al.* 2007, SPITZER *et al.* 2009).

For a successful conservation practice, a deep understanding of the requirements of the species is needed. It has long become clear that larval resource requirements play a key role in butterfly population dynamics, and adults influence population dynamics less by resource requirements, and more by dispersal (THOMAS *et al.* 2011). These two observations of butterfly population dynamics have led to recognition of the importance of habitat quality (DENNIS & VAN DYCK 2003; DENNIS *et al.* 2006; TURLURE *et al.* 2010) and to the conception of metapopulation theory (HANSKI 1999).

Factors effecting population size and persistence: metapopulation theory

Generally, two main approaches exist to explain variation in the population size of butterfly species: metapopulation theory and the habitat quality approach (THOMAS *et al.* 2001). Butterfly habitats in modern landscapes are often fragmented: patches of suitable habitat are surrounded by inhospitable areas and local subpopulations are connected by dispersal. The dynamic of extinction and recolonisation of subpopulations can form a spatially structured metapopulation, where dispersal among local populations has an effect on local dynamics (HANSKI & SIMBERLOFF 1997). In a classic metapopulation, extinction and recolonisation exist in equilibrium (HANSKI 1991), but conservation studies show that this balance is often biased towards decline (VAN STRIEN *et al.* 2011).

Metapopulation studies frequently use butterflies as model species, and the theory has developed itself through butterfly studies (e.g. HANSKI *et al.* 1994; THOMAS *et al.* 1996; HANSKI *et al.* 2000; BAGUETTE & SCHTICKZELLE

2003; SCHTICKZELLE *et al.* 2006; DOVER & SETTLE 2009; VAN STRIEN *et al.* 2011). Metapopulation theory assumes that patch size and isolation are the main factors that influence population size and persistence in a habitat patch (HANSKI & GLIPIN 1997). Persistence and abundance of species with high sensitivity to fragmentation can be described well by a metapopulation structure (e.g. THOMAS & HANSKI 1997; HANSKI 1998; ÖCKINGER 2006; NOWICKI *et al.* 2007; HOVESTADT *et al.* 2011). For some butterfly species, the classic metapopulation structure can be applied (HANSKI *et al.* 1994; WAHLBERG *et al.* 2002), where, either naturally or by the result of habitat loss and fragmentation, the population structure is close to the ideal metapopulation at equilibrium. In other cases, the spatially structured population is slightly different from a metapopulation in equilibrium. High patch occupancy, low rate of colonisation and extinction of local populations are frequently experienced in real butterfly populations (VAN STRIEN *et al.* 2011). This is often the case in declining populations in fragmented environments, which are often the focus of conservation studies and maintaining efforts.

The metapopulation approach has some limitations in continuous landscapes, where the definition of habitat patches is not exact and resources of butterflies are spatially separated (DOVER & SETTELE 2009). The resource limitation approach offers an alternative to avoid the problems of patch definition, continuity of landscapes and sparse location of resources in the matrix (DENNIS *et al.* 2006). This approach determines the extent of habitat based on necessary resources, and emphasises the importance of the habitat quality (VANREUSEL & VAN DYCK 2007). Such studies analyse habitat

quality in light of the habitat requirements of a certain species (OOSTERMEIJER & VAN SWAAY 1998; SKÓRKA *et al.* 2007).

Habitat quality can be described by structural factors, such as the amount of shade or light intensity (GRUNDEL *et al.* 1998), the main components of vegetation and foodplant density (BATÁRY *et al.* 2007), or by the prevalence of nectar sources (FISCHER 1998). Females and males can have different habitat requirements due to their different drivers, such as finding suitable sites for oviposition or mating partners (MUNGUIRA *et al.* 1997; GRUNDEL *et al.* 1998). Vegetation management can also influence the quality of habitats- and therefore the habitat use of butterflies (SMALLIDGE & DONALD 1997).

Habitat quality requirements can differ according to the given life stages, as these different stages require different resources (DENNIS *et al.* 2006). In themselves, the distribution and density of adult butterflies are not necessarily good predictors of ovipositing sites (DOVER & ROWLINGSON 2005), because habitat requirements for eggs and larvae are usually narrower than those of adults alone. Therefore, these life stages essentially determine the distribution of butterfly species (THOMAS 1991; KONVIČKA *et al.* 2003; ELLIS 2003, THOMAS *et al.* 2011).

The occurrence of a butterfly species can be significantly affected by both spatial geometric factors and quality of the habitat (THOMAS *et al.* 1992; WAHLBERG *et al.* 2002). While some studies have considered patch geometry as the most relevant factor (HANSKI *et al.* 1996; THOMAS & HANSKI 1997; NOWICKI *et al.* 2007), other studies have revealed that within-site variation in habitat quality is more important in predicting patterns of site occupancy (THOMAS *et al.* 2001; FLEISHMAN *et al.* 2002). Using a

combination of spatial and habitat quality approaches in the same study enables predictions of population size or density (THOMAS *et al.* 2001; SAWCHIK *et al.* 2003; RABASA *et al.* 2008), and in some cases patterns of site occupancy, more reliably than by their conventional separation (LENDA & SKÓRKA 2010; SANFORD *et al.* 2011).

Conservation status of three protected butterfly species

In this study, I discuss three important aspects of butterfly conservation: the significance of ecological studies on butterfly conservation, the importance of habitat use and availability of resources in all life stages of butterflies, and the consequences of the spatial structure of populations. Instead of analysing all of these aspects in relation to one species, I examined three different species: *Maculinea (Phengaris) teleius* (Bergsträsser, 1779), *Coenonympha oedippus* (Fabricius, 1787) and *Zerynthia polyxena* ([Denis & Schiffermüller], 1775). All three are protected species, although they are threatened to different degrees. The studies aimed to reveal the points where conservation management has an impact upon the long-term survival of the species, and, primarily, to reveal the habitat use and requirements of the species in all cases.

VAN SWAAY (2014) describes five pillars of butterfly conservation: (1) distribution, (2) trends of population size and distribution, (3) drivers of change, (4) conservation actions and (5) communication. In my PhD thesis, I focus mainly on the foundations of conservation actions and the habitat requirements of each species, giving also partial attention to the distribution and abundance of the examined species. Among the species studied, the

extent of initial knowledge differed, from the well-known *M. teleius* to the less studied *C. oedippus* and the under-studied *Z. polyxena*. These butterfly species have different life cycles, habitat requirements and responds to environmental changes.

Habitat requirements and status of *Maculinea teleius*

Maculinea butterflies are among the most intensively studied species due to their special life cycle and endangered status, and because they are sensitive indicators of environmental changes (SETTELE *et al.* 2005). Numerous publications deal with the ecology and conservation of *M. teleius*, some even on possible effects of management. One recent large-scale study on habitat requirements in Germany (DIERKS & FISCHER 2009; and another on metapopulation dynamics in Poland (NOWICZKI *et al.* 2014), review the relevant publications on the topic. Threats such as abandonment of traditional agriculture and habitat loss endanger the species in Hungary, although there are still several large populations (VAN SWAAY & WARREN 2003). The species is well studied in Hungary, the local population structure (KŐRÖSI *et al.* 2012), effects of management on population (KŐRÖSI *et al.* 2014), host ant species (TARTALLY 2008) and genetics (PECSENYE *et al.* 2007) have been surveyed. It is proven that habitat management to strengthen the *Maculinea teleius* populations should be adapted to local site conditions, as host ant species and local climate severely affect the results of different management regimes on similar *Maculinea* species (THOMAS *et al.* 1998).

M. teleius breeds in wet meadows and oviposits in the flower heads of its foodplant, the Great Burnet (*Sanguisorba officinalis* L.). Therefore, the butterfly's distribution strongly depends on the distribution of this host plant (THOMAS 1984). The species is obligatory myrmecophilous (THOMAS *et al.* 1989) with considerable local/regional variations of the host ants (TARTALLY & CSŐSZ 2004; TARTALLY 2008): the host ant species in the study area is *Myrmica scabrinodis* Nylander 1846. Young caterpillars, after developing in the flowerheads of *S. officinalis*, are adopted by their host ants (THOMAS 1984). In the ant nests the caterpillars live as social parasites; that is, they prey on the ant brood until they complete their development the following year. FIGURNY & WOYCIECHOWSKI (1998) observed that *M. teleius*, in contrast to the sympatric species *M. nausithous*, oviposits on the younger and shorter flower shoots that are closer to the ground and have fewer flowers. The abundance of flowerheads can be greatly affected by management (JOHST *et al.* 2006). *Maculinea* populations only persist if the niches of foodplant and host ant overlap (THOMAS *et al.* 1998).

Habitat requirements and status of *Coenonympha oedippus*

Coenonympha oedippus is a species distributed in the Palearctic steppe zone (BOZANO 2002). The European populations declined or extinct and are threatened in several countries. There are large and stabile populations in Italy (BONELLI *et al.* 2010), large but threatened and highly isolated populations exist in Croatia (ŠAŠIĆ 2010) and Slovenia (ČELIK & VEROVNIK 2010). The European populations generally occupy semi-open wet habitats: *Molinia coerulea* meadows, bogs, wet heathlands, sedges of swamps and

11

forest meadows (DOLEK *et al.* 2010). There are some populations in the Mediterranean parts of Europe that occur in dry habitats (ČELIK 2004; VAN HALDER *et al.* 2008), but also with a high coverage of *Molinia coerulea*. *Molinia* and *Carex* species are the main foodplants of the polyphagous larva (BRÄU *et al.* 2010).

It is one of the most endangered butterflies in Europe; it is considered as nearly threatened by IUCN (2011) and is listed in Annexes II and IV of the Habitat Directive (1979) and Annex II of the Bern Convention. The geographical distribution of the species is highly fragmented and colonies are isolated (KUDRNA 2002). Most recent studies on the distributions, population sizes and reproduction biology of the species were included in a special issue of the journal Oedippus (DOLEK *et al*. 2010). One of the first publications about the species describes its weak, jumping flight (SEITZ 1906), which is related to its supposed weak dispersal ability (LHONORÉ & LAGARDE 1999; ČELIK *et al.* 2009). LHONORE and LAGARDE (1999) mention the problems of fragmentation, isolation and other threatening factors that endanger the long-time survival of the butterfly.

European populations are threatened with habitat loss and degradation, especially land drainage, abandonment and changes in habitat management. Populations also suffer from the spread of invasive weeds (*Solidago* spp.) and encroachment of bushes after abandonment, collection of butterflies, development of built-up areas and climate change (VAN SWAAY & WARREN 1999; ČELIK & VEROVNIK 2010; ÖRVÖSSY *et al.* 2010; ŠAŠIĆ 2010). In Eastern European wet meadows, *Solidago* spreads forcefully and negatively affects butterfly communities (MOROŃ *et al.* 2009).

In Hungary, remarkable populations were described in the Hanság, Kiskunság and Óbuda regions, as well as in Szár (BÁLINT *et al.* 2006). These habitats disappeared due to large-scale drainage (MOLNÁR *et al.* 2008) and urban development. Two habitats remained in Hungary, a permanent population in the Kiskunság region, near Ócsa (BÁLINT *et al.* 2006) and in the Fertő-Hanság region.

Fortunately, during our study, two exciting developments were identified. We found several subpopulations around the known location, which released the threat of short-term extinction of the species. While we focused on the known area, another research group found a population in a geographically distinct region, in the Fertő-Hanság National Park (AMBRUS, pers. comm.).

The nearly threatened status of the species motivates the monitoring of its population size. Efforts to maintain the small and isolated populations by conservation management are hampered by a lack of knowledge about the habitat requirements of this species. Hence, a suitable management regime would halt further decline and support the long-term survival of the species. Development of a proper management action plan should be based on a survey that describes which factors influence the metapopulation structure of the species under consideration and determines the parameters of the best available habitat quality.

Habitat requirements and status of *Zerynthia polyxena*

Z. polyxena is not strongly threatened, but is protected. It shows trends towards decline in several European locations and is already extinct in

Germany and Switzerland (VAN SWAY *et al.* 2010a). The species is listed in the Habitat Directive Annex IV and the Bern Convention Annex II. No specific conservation actions are needed at the European level, but in countries where the species is in decline, important habitats should be protected and managed. Butterfly Monitoring Schemes (VAN SWAAY *et al*. 2010b) should monitor the effects of management. The presence of early succession stage of the natural habitat depends on the presence of natural or human disturbance. Allowing the turnout of natural disturbances, such as flooding or low-intensity human disturbance, can help to maintain their habitats. There is only one publication about the population structure of this species (ČELIK 2012) our study on egg distribution adds to this (BATÁRY *et al.* 2007). *Z. polyxena* populations in Hungary are widespread and are not in immediate danger. The species may require management actions to preserve its current populations.

AIMS

Maculinea teleius

Our aims in **Study I**. were to describe the microhabitats available for *M. teleius* in the mosaic of fens and meadows in an extensively grazed area, to determine the factors that influence the presence and density of *M. teleius* and finally to investigate the relationship between host ant and *M. teleius*.

Coenonympha oedippus

The aim of **Study II.** was to estimate some essential parameters of population dynamics (population size, sex ratio, survival rate, lifespan) in a single population of *C. oedippus* using mark–release–recapture method.

In **Study III.** our aims were to gain information about the population structure of *C. oedippus*: discriminate clusters based on phenology, asynchrony of subpopulations and movement pattern of the species, and to determine whether and how habitat quality affect its population size and density.

Zerynthia polyxena

The aims of **Study IV.** were to determine factors affecting the small-scale habitat use of *Z. polyxena*, including the distribution of adults, eggs and larvae among foodplant patches, and to reveal the resource requirements of the species in all life stages in a human-dominated landscape. We hypothesized that structural differences of foodplant patches in different vegetation types has an effect on distribution and abundance of *Z. polyxena*.

MATERIAL AND METHOD

The methods and results are available in detail in the attached publications.

Study species

M. teleius population is coexsisting with *M. alcon* at Kunpeszér. The population is divided into smaller subpopulations due to the mosaic landscape. Population sizes of *M. teleius* are generally sufficient, but it is sensitive to environmental changes. The habitat of the local population is maintained by grazing. The flight period is in August.

C. oedippus population at Ócsa in the Kiskunság region was considered to be at high risk of local extinction due to habitat deterioration and isolation, as the result of drainage, abandonment of management and dispersion of invasive plant species. The species presence was sporadically monitored in one of the Ócsa habitats in the 70', but without detailed studies.

Z. polyxena's larval foodplant is *Aristolochia clematitis* L., females lay their eggs in clusters on the leaves of the host plant. The hatching larva feeds on the leaves and concentrates the toxins of the plant in its body. Hence, the larva and the adult are toxicuous, brightly coloured and easy to recognise. The studied population lives in tree plantations. The main threatening factor for the butterfly is the disappearance of the foodplant, due to too intensive management or the lack of disturbance.

Study sites

Study sites of *M. teleius*

　　M. teleius population was studied at Kunpeszér, on the Hungarian Great Plain. The area is a mosaic of fens and meadows. The patchiness of the area is due to the variation in local topography affecting soil humidity. Fens, situated in the most humid and deepest depressions, are characterised by willow bushes and reed, the deepest parts are not suitable habitats for this butterfly, but the edges are ideal habitats. Eight fens of a comparable size were selected (mean = 2.8 ha, range = 0.8–5.4 ha) (Fig. 1. in **Study I.**). Around these depressions, four types of microhabitat were available for this butterfly: *Typha-*, *Lythrum-*, *Stachys-*, *Molinia* microhabitat (**Study I.**). Cattle (0.3 cows/hectare) had grazed in the study area for at least 5 years from early spring until late autumn. The grasslands were never fertilised or treated with pesticides.

Study sites of *C. oedippus*

　　C. oedippus was studied at an area next to the town of Ócsa. In **Study II.** we focused on a small (0.65 ha) habitat patch for population size estimation. In **Study III.** we enlarged the study area and covered all occupied patches of the habitat complex. The species' presence was recorded in 16 patches with 12 patches of higher densities. These twelve patches were isolated from each other by 0.01–3.2 km, separated by softwood forest groves, shrubs, grasslands or agricultural areas (Fig. 1. in **Study III**.). They varied in size from 0.14 to 1.66 ha. The examined patches were all wet meadows with the ground water level close (0.1–2.0 m) to the surface, and vegetation was

17

dominated by mainly *Molinia coerulea subsp. altissima* (heterotypic synonym of *Molinia arundinacea* Schrank) and other *Poaceae* and *Carex* species with few nectar sources for the butterflies (Örvössy *et al.* 2010). The traditional management of the area was extensive mowing for haymaking. Most of the studied patches had been abandoned and experienced weed invasion and scrub encroachment. Traditional once a year mowing is still carried out only in three patches.

Study sites of *Z. polyxena*

One of the biggest *Z. polyxena* populations in Hungary lives in the habitat near Csévharaszt. Black locust and poplar tree plantations cover the area altering with open clearings and artificial linear hummocks (Fig 1. in **Study IV.**). These hummocks were created during plantation management; stumps of harvested trees were merged to a line and covered with soil. Hummocks were partly shaded and disturbed and were ideal habitats for the butterfly's foodplant (*Aristolochia clematitis*).

Sampling design and methods

In **Study I.** and **IV.** we used transect counting for estimating relative abundance, while in **Study II.** and **III.** we used the mark-release-recapture method for estimating population size. Transect counting is a quick method, applicable on adults and larvae without handling effect, relative abundance data are suitable to compare distinct sites. Mark-release recapture technique is frequently used during butterfly population size estimation while describes population structure. The daily survival rate, probability of

catching, daily population size, life expectancy and total population size can be estimated and the dispersal among patches can be examined.

STUDY I.

Altogether 40 transects (divided into ten quadrates) were laid out around eight marshland fens (Fig. 1. in **Study I**.). Number of *M. teleius* butterflies was noted. During the flight period the number of foodplant flowerheads was counted, soil humidity and vegetation height was measured, and microhabitat type and grazing intensity (absent, light or strong) was classified in every quadrate. Pitfall traps were used to detect the presence of host ant species.

STUDY II.

Mark–release–recapture method was used in one habitat patch in 2005-2007 (patch "MV" in Fig 1. in **Study III.**). Sampling was conducted daily in 2005 and 2006, while every second day in 2007. A grid of 5×5 m was laid down to locate captures. The survival and capture probability were estimated for both sexes with the Cormack–Jolly–Seber method using Mark 5.1 (WHITE & BURNHAM 1999). The best models were selected based on Akaike's information criterion (AIC). Mean lifespan was calculated from survival probability (COOK *et al.* 1967). The daily population size was estimated with program POPAN 5 (ARNASON & SCHWARZ 1999). The total size of butterflies in a year was calculated with the modified method of COOK *et al.* (1967).

STUDY III.

We carried out mark-release-recapture survey in twelve habitat patches in 2007. Each patch was visited every other day. Sampling effort was standardized. Four additional locations were included in the Virtual Migration 2 model. We measured the quality of each habitat: height of vegetation, height of grass litter, number of flowers/nectar sources, area covered by tussocks, percentage of bush cover, groundwater level.

STUDY IV.

To estimate *Z. polyxena* density in the four vegetation category (poplar, black locust, clearings, hummocks) 23 large foodplant patches were selected for sampling (Fig. 1. in **Study IV**.). Number of adults was counted altogether 16 times. Transects were visited in altered order to avoid effects of timing. Number of eggs and larvae was counted twice in each plot, first in the middle of the flight period than after larval hatching. Number and height of foodplants, height of other plants and percentage of bare ground were measured. Light intensity was measured on each transect, at the second survey by LI-189 Quantum/Photometer.

Data analysis

STUDY I.

Logistic regression analysis was used to determine the relationship between presence of butterflies and explanatory variables. A nested design was used with transects nested within fens and quadrates within transects. Explanatory variables were the number of foodplant flowerheads as the first

covariate, fen and transect as random factors, then, one by one all variables (soil humidity, grazing category, microhabitat type and vegetation height) were added until the best model (smallest AIC value) was obtained. Correlation between the quadrates was built into the models, which were nested in transects to avoid edge effects causing bias in the models.

Linear regression analysis of fen "A" included number of butterflies/quadrate as the dependent variable, foodplant flowerheads, transect as a random factor and quadrate correlation. The comparisons between microhabitat types and distance from the fen, soil humidity, flowerhead density and vegetation height were tested using the Kruskal-Wallis test. The relationship between the number of *M. teleius* and *Myrmica scabrinodis* was analysed using a Mann-Whitney test. All statistical analyses were performed using R software packages (R DEVELOPMENT CORE TEAM 2004).

STUDY II. and STUDY III.

We estimated the population size for only one habitat patch of *C. oedippus* at Ócsa in **Study II**. We used Cormack-Jolly-Seber (CJS) model to estimate the population parameters for each year of the 3 years survey. Survey of 2007 was also used in the analysis of **Study III**.

In **Study III**. we surveyed more habitat patches. The mark-release-recapture dataset was analysed in two steps, and separately for each of the twelve habitat patches. First, we fitted a Cormack–Jolly–Seber (CJS) model to each dataset with time- and sex-dependent parameters (survival rate and recapture probability). We tested for the goodness of fit by a bootstrap GOF

test and a v2-based GOF test ('Release') (LEBRETON *et al.* 1992). Then we performed a model selection based on AIC values to reach the most parsimonious model (BURNHAM & ANDERSON 2002). Secondly, we fitted a Jolly–Seber (JS) model with a set up for survival rate and encounter probability as in the most parsimonious CJS model. Model selection was performed again to find the best parameterization (the JS model had two additional parameters: population size N, which can be sex-dependent, and proportional recruitment pent, which can be time- and sex-dependent). Daily population size was a derived parameter of the JS model. Average lifespan was calculated from the survival rate of the CJS model (1/-ln(Phi), COOK *et al.* 1967). All analyses were carried out using MARK 5.1 software (WHITE & BURNHAM 1999).

The Virtual Migration 2 programme (HANSKI *et al.* 2000) was used to estimate the following dispersion and population parameters for both sexes: within-patch mortality, migration rate per one-hectare patch, scaling of migration with patch size, distance-dependence of migration, mortality during migration and scaling of immigration into a patch.

The relationship between butterfly quantity and habitat quality parameters was analysed with ''General Additive Models, for Location, Scale and Shape'', without any smoothing effect, only for exploiting the availability of lognormal error distribution. Two response variables were used in the analyses: total population size and the maximum observed density of individuals. Predictor variables were standardized: height of vegetation, height of grass litter, number of flowers/nectar sources, area covered by tussocks, percentage of bush cover, area and groundwater level.

We applied a backward-stepwise model selection based on AIC values. These analyses were performed using gamlss package (STASINOPOULOS *et al.* 2012) of R 2.12.2 statistical software (R DEVELOPMENT TEAM 2011).

STUDY IV.

Due to the overdispersion and heteroscedasticity in our dataset, and correlations among explanatory variables, we used conditional inference trees to analyse our data. We carried out six regression tree analyses with quad type test statistic and Bonferroni correction. Number of adults, eggs and larvae as response variables were analysed separately. In the first three trees explanatory variable was only the vegetation category, while in the other three trees we used undergrowth parameters as explanatory variables: height of foodplants, number of foodplants, height of other undergrowth plants, percentage of bare ground and (only in the case of adults) light intensity. Conditional inference trees are not sensitive to the association between explanatory parameters, as the hierarchy of the outcome can show the connection among them. We also included the transect ID that each plot belonged to. Undergrowths parameters by vegetation type were tested by Kruskal-Wallis test and Multiple Comparison after Kruskal-Wallis test. Correlations of the undergrowth parameters with light intensity were tested by Spearman correlation tests. We used R for statistical analysis (R DEVELOPMENT CORE TEAM 2011); the party package was used for conditional inference tree analysis (HOTHORN *et al.* 2006), the pgrimess (GIRAUDOUX 2014) package was used for Multiple Comparison after Kruskal-Wallis test.
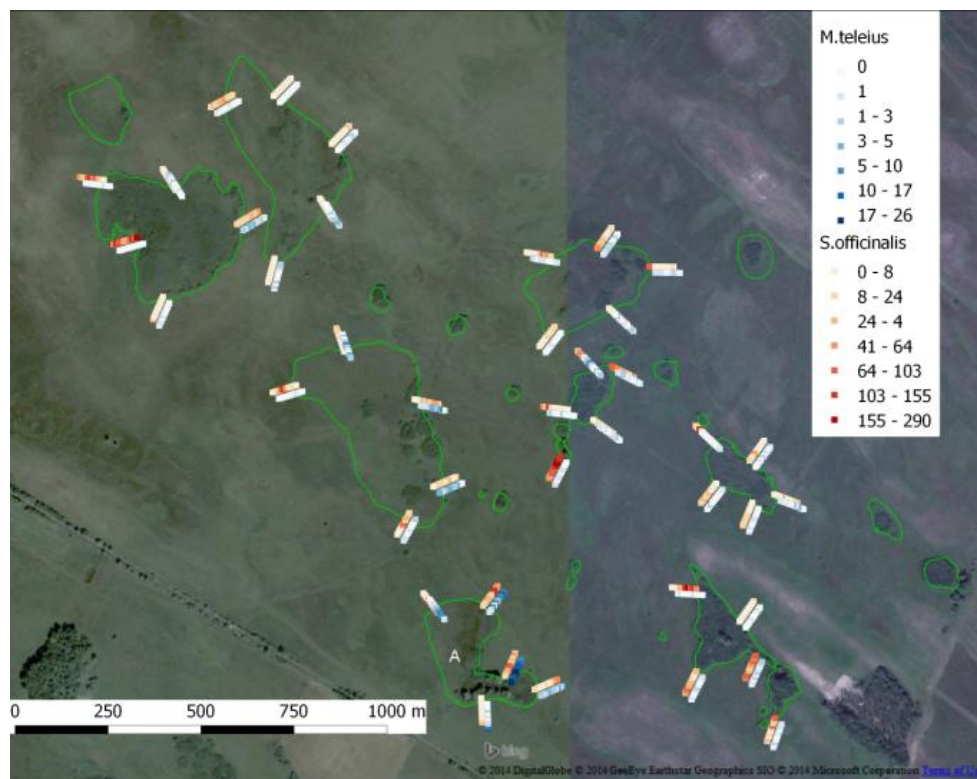
RESULTS

Study I.:

Presence of *M. teleius* was related significantly to the microhabitat type in **Study I.** Altogether, there were 553 individual sightings of butterflies, 290 were at the most populated fen (fen "A", Figure 1.).

Figure 1. Abundance of *M. teleius* and *S. officinalis* in the quadrates.

The best nested logistic regression model showed a significant effect of microhabitat type, but no effect of foodplant or grazing (Table 1). *M. teleius* seemed to prefer *Stachys* and *Molinia* microhabitats, where the butterfly was recorded in more of the quadrates, than in the *Lythrum* and *Typha* microhabitats, which were less preferred (Fig. 3).

Abundance of *M. teleius* was significantly related to the number of foodplant flowerheads but not to grazing (Table 1.). The abundance of *M. teleius* increased with the number of flowerheads (Table 1, Fig. 4). Over the whole area the number of *M. teleius* was significantly higher in quadrates where host ants (*Myrmica scabrinodis*) were present compared to quadrates lacking the host ant (Mann-Whitney test, $U = 2612.5$, $p = 0.003$).

The position of the microhabitat types depended on the distance from the fen, usually in the order *Typha* microhabitat (edge of the fen), *Lythrum* microhabitat, *Stachys* and *Molinia* habitat. This distribution was not rigid, as some of the microhabitats were not present or not in this order. There were significant differences in the distances of four microhabitats from the edge of the fens (Kruskal-Wallis test; $\chi^2 = 55.2$, d.f. $= 3$, $p < 0.001$), in soil humidity (Kruskal-Wallis test; $\chi^2 = 176.6$, d.f. $= 3$, $p < 0.001$) and vegetation height among microhabitats ($\chi^2 = 235.4$, d.f. $= 3$, $p < 0.001$). The highest vegetation was at the edges of fens and declined along the transects as microhabitat types changed (Fig. 2b in **Study I.**). The foodplant flowerhead density was significantly higher in the *Lythrum* and *Stachys* than in *Typha* and *Molinia* microhabitats ($\chi^2 = 62.1$, d.f. $= 3$, $p < 0.001$).

Study II.:

This study shows the population structure of *C. oedippus* in a habitat patch during a three year period. The population was moved from the originally known location and was found in an adjacent, but deeper area, probably due to desiccation of the area. The estimated total population size was 137 in 2005, 273 in 2006 and 212 in 2007 (Tables 1 and 2). The population structure parameters are in Table 2.

The highest estimated daily population size varied between 45–81 for males and 29–96 for females (Fig. 2). Males reached their maximum estimated daily population size earlier than females in each year. The butterfly showed the characteristics of protandry, males outnumbered females in the first days of the observation period (Figs. 2 and 3).

The model selection resulted gender dependent survival and capture probability in the first two years and gender independent survival and capture probability in the third year. Female survival probability was slightly higher than that of the males in 2005 and 2006. The survival probability in the third year was gender independent and decreased to 0.78. The mean lifespan of females was 8.58 and 7.18 days in the first years, while mean lifespan of males was 5.74 in 2005 and 5.04 in 2006. The mean lifespan had decreased to 3.95 for both sexes in 2007 (Table 2). Capture probability was 0.40 and 0.53 in males and 0.22 and 0.38 in the case of females in the first years and 0.27 in 2007 (Table 2).

Observations of individual movements during the sampling suggested the individuals were sedentary; their flight was short and jumping. The average

26

distance between consecutive recaptures was 38.3 m (52 animals, 1–11 movements/individual). According to the tracking data of individuals, males moved more frequently and flew longer distances (approx. 10–15 m/occasion) than females (0.2–4 m), although sample size was not sufficient for statistical analysis.

Study III.:

While we carried out intensive mark-release study in the already known habitat patch, we also mapped the potential habitats in the area. Sixteen locations were found. We attempted to estimate the whole population system's size. In 2007, the most promising 12 patches was regularly visited and a mark-release study was carried out.

The estimated total number of individuals in the studied population system was slightly over 3,000, which was calculated for ten habitat patches, where the total estimated number of individuals varied between 24 and 1055. Two groups of patches were separated by relatively large distances and differed in size (Fig. 1), peak of daily population size was also 6 days from each other in the two groups of patches. Altogether, 1,496 butterflies (914 males and 582 females) were marked, during 2,052 capture events. Total population size per patch varied between 24 and 1,055 individuals, the maximum daily butterfly density ranged between 0.09 and 1.72 observed individual per minute per patch (Table 1.) The daily survival (SE) varied between 0.22 (0.18) and 0.79 (0.02) for males and 0.82 (0.04) and 0.87 (0.08) for females (Fig. 2.). In all patches protandry was observed,

27

i.e. males emerged earlier than females (Fig. 2.). Average lifespan (SE) varied between 0.7 (0.5) and 7.3 (0.3) days (Table 1.).

Altogether, 48 dispersal events (37 males and 11 females) were detected. Females moved less frequently and shorter distances than males. For males, the longest observed movement was 5.8 km, while the longest observed movement by a female was less than 0.5 km. The Virtual Migration 2 model showed that one dispersal parameter differed significantly between males and females; distance-dependence of migration was stronger in the case of females (Table 2).

We also aimed to find connection among environmental characters and size of the local populations and density of those populations. The maximum daily density was significantly affected by the groundwater level and by the area covered by tussocks following the minimal adequate general additive model (Table 4). The density of butterflies was higher in habitats with lower groundwater level, and with larger area covered by tussocks. The population size was larger in habitat patches where the groundwater level was lower and the grass litter was higher, both parameters had almost equal influence on population size based on general additive model (Table 4).

Study IV.:

Z. polyxena adults used the foodplant patches in all of the four vegetation types, but their distribution was uneven (Fig. 2). Altogether 182 butterflies were observed during 16 sampling occasions along the 23 transects. Number of adults was significantly lower in poplar plantations than in other types.

28

Number of butterflies was significantly higher in transects with smaller percentage of bare ground. Number of food plants had a marginally significant positive effect on butterfly numbers where bare ground cover was >25% (Fig. 3).

922 eggs were counted after the peak of the flight period. Eggs were present in 28 out of the 115 sampling plots. Number of eggs was only marginally significantly higher in black locust and hummock plots than in open and poplar plots (Fig. 3). The result of 'conditional inference tree' analysis with the undergrowth parameters as explanatory variables showed, that plots with higher than 45 cm host plants hosted significantly more eggs than plots with smaller host plants. Host plant number significantly partitioned plots with smaller (<45 cm) host plants into two groups; plots with more than 135 host plants hosted more eggs than plots with fewer plants (Fig. 3).

471 larvae were counted in 48 of the 115 plots. Larvae number was significantly higher in plots of hummock vegetation than in other types. The second, marginally significant node of the conditional inference tree partitioned black-locust and open plots from poplar plots. The regression tree with the undergrowth parameters showed that foodplant height partitioned the sample into three categories. Plots with higher than 75 cm foodplants had the highest number of larvae, fewer larvae were in plots with foodplants between 60-75 cm, and the lowest number of larvae was in plots with shorter than 60 cm foodplants (Fig. 3).

The four vegetation types differed in number of foodplants, height of foodplants, cover of bare ground and light intensity (Table 1). Foodplant height, number, and light intensity were the highest in hummocks, while bare ground cover was the highest in poplar habitat. Height of undergrowth during egglaying was significantly higher in black-locust and hummock than in open and poplar quadrates. There was a negative correlation between light intensity and percentage of bare ground cover, while we found a positive correlation between light intensity and number of host plants in the first survey (see results of Kruskal-Wallis test and comparison after Kruskal-Wallis test in **Study IV.**).

DISCUSSION

All of these studies aimed to reveal the habitat use of protected butterflies, the optimal and the available quality of habitats and its effects on population size and density. Habitat quality can vary within the examined habitat patch or patch complex. Butterfly populations react to these differences, avoid unsuitable places and persist in large numbers where environmental parameters are the most suitable. Because all of the examined study sites are under some form of human management, it is crucial to understand what combinations of environmental parameters are best and worst for species, especially when the population of species is in immediate danger of local extinction. Shaping existing management based on knowledge regarding the local populations' habitat requirements could be sufficient in supporting the long-term survival of these protected butterflies.

M. teleius is a well-examined species throughout Europe, but the local populations have different requirements due to environmental conditions, climate and host ant species. In a large mosaic landscape, the microhabitat type primarily determined the presence of *M. teleius* imagos. The highest number of *M. teleius* was observed in *Stachys* and *Lythrum* microhabitats. The lack of foodplant effect on this scale is probably the result of the availability of foodplant on the entire study area. The abundance of *M. teleius* in fen "A", however, was influenced by flowerhead density of *Sanguisorba officinalis*. The foodplant density differed in the microhabitats with the highest density occurring in *Stachys* and *Lythrum* microhabitats.

31

The drier and shorter *Molinia* microhabitats, which were generally farthest from the fens, and the wetter and higher *Typha* microhabitats close to the fens, probably simply act as a matrix for the butterflies. Similar to our results, THOMAS & ELMES (2001) found that the foodplants preferred by *M. teleius* were most abundant in short (0–30 cm) vegetation in France and Poland. In the *Stachys* microhabitat, the range in vegetation height was 10–36 cm for the whole area; in the *Lythrum* microhabitat, it was 22–44 cm. Therefore, the butterfly species in this region seems to have similar vegetation height requirements to other parts of Europe. Similar to our results, a German study shows that *M. teleius* abundance is positively related to foodplant density, vegetation height and host ant availability (DIERKS & FISCHER 2009). In contrast to our results, NOWICKI *et al.* (2005a) found that, at a metapopulation level, foodplant density does not limit the abundance of *M. teleius*. In our study, microhabitat types likely have direct and indirect effects on butterfly abundance throughout microenvironmental factors. The present study did not indicate that different local grazing intensity had a direct effect on butterfly occurrence or abundance. Nonetheless, we have to admit that the local grazing and trampling intensity is very low (less than 0.3 cow/ha). Unlike other studies (e.g. GRIEBELER & SEITZ 2002; WALLIS DE VRIES 2004), we did not compare sites with different grazing intensity or regimes, because the entire area was subject to the same management. However, grazing was uneven on the area; different levels of grazing intensity occurred due to the daily routes of the cattle herd. Despite these caveats, the generally low grazing pressure recorded is

probably adequate management for this study site. Like others (GRIEBELER & SEITZ 2002), we also believe that grazing results in a particular vegetation height and cover of grassland favourable for the butterfly, and especially, its host ants. Abundance was significantly higher in quadrates where the host ant was present. Though this study is too limited to determine if this butterfly is directly or indirectly affected by the presence of host ants, we draw attention to the fact that lower host ant density can increase the risk of local extinction (THOMAS 1994). VAN DYCK et al. (2000) argue that egg distribution of *Maculinea alcon* differs from random, and host ant presence may influence it. However, most studies do not find a significant relationship between host ant presence and abundance of *Maculinea* imagos or eggs (e.g. BONELLI et al. 2005; MUSCHE et al. 2005; NOWICKI et al. 2005b; but see ANTON et al. 2005; GLINKA & SETTELE 2005). VAN DYCK et al. (2000) suggest that the egg distribution pattern observed at the end of the egg-laying period may mask the relationship between host ant presence and early egg laying. Therefore, for the conservation of this endangered species, it is important to maintain the quality of the remaining habitats (MAES et al. 2004; WALLIS DE VRIES 2004; JOHST et al. 2006). The implication for conservation is that low intensity grazing should be continued in order to maintain the current distribution of microhabitats. Our work thus has contributed to the recommendations for managing Habitat Directives areas (VAN SWAY et al. 2012).

C. *oedippus* is a less studied species, but its conservation status is threatened in many countries. The first results of the population size

estimation on the known habitat showed that there was no major fluctuation in population size during the three-year study period. The variance coefficient of population fluctuation was 0.31 for three years, which is in the lower region of butterfly populations (FRANZÉN *et al.* 2013). This finding gives a promising sign regarding its survival even though long–term trends cannot be estimated with this time scale.

Along with ČELIK's survey (2004) in Slovenia, protrandric population structure was observed. Both males' and females' movement was restricted to short distances within the habitat patch, similar to ČELIK's results. Short flights imply sedentary living habits and closed populations, the assumption of closed populations was partially disproved in the latter **Study III**.

The apparent survival rate (0.78–0.89) of the species is in the higher range for butterflies. A survival probability of around 0.8 is typical to butterfly species with a colonial population structure in temperate climate zones (BRAKEFIELD 1982). Butterfly species with high daily survival rates are prone to being sedentary with limited dispersal ability, making them vulnerable, like *Euphydryas aurinia* (SCHTICKZELLE *et al.* 2005) or *Lopinga achine* (BERGMAN & LANDIN 2002). During 2005 and 2006, the survival rate of the females was higher than that of the males, which is in agreement with the results of ČELIK (2004). A decline in the female survival rate in 2007 is a reason to worry, as the shorter lifespan of females can have a direct effect on the quantity of eggs laid. In the case of xerophilous ecotype of *M. alcon*, it has been proven that the total quantity of eggs possibly laid can be many times higher than the realized number of eggs laid; in other

words, the females are time-constrained in terms of egg laying (KŐRÖSI *et al.* 2007). Along with the decreased lifespan, the number of laid eggs probably decreases, making the basis of the next generation and the long-term survival of the population uncertain. However, the decline of the apparent survival rate can be a sign of growing dispersion; dispersion may occur because of the declining quality of the habitat patch or any other general problem, such as the unusually hot weather in June and July of 2007.

The mean lifespan of males was 5 to 6 days and females 7 to 9 days in the first years, which is slightly higher than estimated in the Slovenian population. However, in 2007, the mean lifespan was similar to the Slovenian results (ČELIK 2004). It is of particular importance that at the beginning of our sampling in 2005, the population was found in a different location, in a deeper site, than during the last surveys of the 80's. In this respect, this fact warns of the danger of continuous desiccation.

Following the initial results of population structure in the examined habitat patch, we explored the area for more possible habitat patches in 2006. From the 16 locations, 12 were promising for holding a population or subpopulation. **Study III** shows that the 12 examined populations form a metapopulation, which is larger both in area and population size than earlier estimations suggested (BÁLINT & MÁTÉ 2004); however, it is divided into small subpopulations, which indicates that the population complex may be vulnerable due to small subpopulation sizes. The attributes of classic metapopulations include colonization-extinction dynamics, fast turnover

rates, sufficient dispersal among habitat patches, asynchronous dynamics of the local populations, and strict distinction between habitat and hostile matrix (HANSKI & GLIPIN 1997; HANSKI 1998; BOURN *et al.* 2000).

Our results suggest that female dispersal is very low; hence, the probability of recolonization is low, and a fast turnover rate is unlikely (HANSKI & GLIPIN 1997). While females move only among the closest habitats, there is evidence that males are able to move between all the examined habitat patches, which is inconsistent with our first foreknowledge on closed populations based on short within-site movements and high daily survival rate (details in **Study III.**). Similar gender differences in dispersal were also observed in an Italian population (BONELLI *et al.* 2010). In a Slovenian habitat complex, the maximum observed dispersal movement was less than 340 m (ČELIK & VEROVNIK 2010), whereas a Croatian study showed no dispersal even among close habitat patches (450 m; ŠAŠIĆ 2010).

Spatial asynchrony in demography of local populations is also frequently detected in metapopulation dynamics (SUTCLIFFE *et al.* 1997). In the studied metapopulation, there were two groups of habitat patches with 6 days difference between the peaks of the estimated daily population sizes. The first peak occurred in the largest, more open patches on the western side of the study area, while the latest peak was in the smaller, more closed habitat patches on the eastern side (Fig. 2. in **Study III**.). In this case, the distance between the two groups and difference between habitat characteristics, such as area and shading, may together have caused the asynchrony among

36

subpopulations. This asynchrony is probably not large enough to save a subpopulation from environmental perturbations, such as unfavourable weather conditions, but it could strengthen the metapopulation, as the two groups of patches are separated by time and distance.

Dispersal among habitat patches is possible, as patches inhabited by the metapopulation have soft rather than sharp habitat boundaries. Several male butterflies were spotted in between habitat patches, indicating that the matrix is suitable for longer persistence; however, female dispersal is more limited. These differences in dispersal distances may result from sex-specific effects of an unfavourable matrix environment on flight speed. Dispersal was not even among patches, and the VM2 model did not fit in some patches. Those patches probably differed in habitat quality, affecting dispersal pressure (BAGUETTE *et al.* 2011).

According to these results, the metapopulation of *C. oedippus* at Ócsa consists of two groups of habitat patches that can aid each other's long-term survival even though we did not observe any female dispersal between the two groups. Female dispersal was limited to very short distances, but male dispersal might have been also controlled by habitat quality, along with patch area and distance. Our results indicate that creating stepping-stones or corridors for females between habitat patches may have a positive effect on female dispersal, and therefore, strengthen the metapopulation.

Habitat patches differed in several ways: area, quality and earlier and current management. Patches of the same size were very different in terms of the number of marked individuals (Table 1 in **Study III.**). While the

37

small number of marked individuals in patch Kb can be explained by its distance from the core habitat patches, the centrally located patch E must be of lower quality as it only supports a small population. In addition, there are differences in the lifespan of males and females among the habitat patches, which can be related to different survival in and dispersal from the patches. Greater dispersal can be caused by several factors, including lower habitat quality, males searching for females and density dependent dispersal (BAGUETTE *et al.* 2011). Overall, male dispersal was greater than female dispersal, explaining the lower apparent survival and shorter lifespan for males. The shorter estimated lifespan compared to other studies (ČELIK & VEROVNIK 2010; ÖRVÖSSY *et al.* 2010) and low recapture rate are probably the consequence of dispersal among local habitat patches.

Determination of habitat quality in the patches and the requirements of the species can help determine proper habitat management, which can facilitate long-term persistence of the subpopulations. Three variables of habitat quality were of particular importance: groundwater level, height of grass litter and the area covered by tussocks. In contrast to our expectation that higher water levels increases habitat quality for the subpopulations, we found that the patches with lower groundwater levels were inhabited by larger and denser subpopulations. However, we have to acknowledge that this phenomenon is only true at this range of groundwater level, as the surrounding drier, uninhabited areas were not included in the study. Conservation efforts were made to maintain or increase the groundwater level in the area after the study period.

The effect of water level rise should be studied on the population of the species as it may have a detrimental effect on larval survival by changing vegetation structure and microclimate. An earlier study on *Coenonympha tullia* showed that larvae could climb up to high positions during flooding (JOY & PULLIN 1996). Therefore, maintaining tall vegetation is important for larval survival in areas subject to flooding. During winter and early spring, the study area can be covered by water, and the existence of dry areas could be crucial for larvae survival.

Local adult *C. oedippus* butterflies may prefer semi-open habitats with bushes (ČELIK & VEROVNIK 2010; ÖRVÖSSY *et al.* 2010; ŠAŠIĆ 2010), because bushes develop well where the groundwater is not too high, providing a better microclimate for the butterflies in hot summers. More specifically, the groundwater level should be high enough to maintain the Molinietum vegetation for the species, but sufficiently low to allow larval survival and the presence of bushes for adult preferences. Although the presence of bushes might increase the size and density of subpopulations, encroachment of bushes due to abandonment of these wet meadows can destroy the habitats in the study area and in other European locations (BRÄU *et al.* 2010; ČELIK & VEROVNIK 2010; ÖRVÖSSY *et al.* 2010; ŠAŠIĆ 2010). Regular mowing can prevent encroachment of bushes and the spread of weeds, such as *Solidago* spp., but it also has a negative effect on tussock structure and the amount of grass litter (BARTOŠ *et al.* 2011).

Structured vegetation with tussocks and large amounts of grass litter were among the most important factors affecting population density and size

in the study area. The maximum daily density was higher in habitat patches where tussocks covered a large proportion of the patch, and the estimated population size increased with the height of grass litter. This could be the consequence of larvae overwintering inside the tussocks and grass litter (BRÄU *et al.* 2010). Traditionally, infrequent (once yearly) mowing by hand in autumn maintained these semi-open meadows. Too frequent mowing could lead to the loss of grass litter and tussock structures, while lack of mowing would result in the area (SKÓRKA *et al.* 2007) becoming overgrown.

In **Study IV,** we demonstrated that the distribution of different life stages of the model species *Z. polyxena* requires slightly different habitats. Although distribution of adults and juvenile forms showed quite similar patterns, we also revealed some differences that can be explained by different environmental conditions in distinct vegetation types.

Adult butterflies clearly avoided poplar patches, but their abundance in the other three vegetation types was fairly similar. This pattern largely coincided with the cover of bare ground, and none of the other environmental variables had significant effects on it. However, we suppose that light intensity may play a crucial role in affecting butterfly movement and distribution. Light intensity was negatively correlated with bare ground cover. It is possible that bare ground cover was influenced by the amount of sunlight on an area during the whole development period of *Z. polyxena*. Our result that bare ground and shaded microhabitat types negatively affected adult abundance confirms the conclusion of ČELIK (2012) that host

plant stands in sunny locations is strongly related to male numbers and weakly related to female adult numbers. ČELIK showed that within the foodplant patch size or amount of foodplant had no effect on imago abundance similar to our study (ČELIK 2012). Foodplant occurred in high amounts and probably was not a limiting factor on the study area; meanwhile, the study did not include areas without foodplants. Some studies show that the availability of larval resources does not affect the abundance of females, e.g. *Parnassius apollo* (FRED *et al.* 2006). However, other large-scale studies suggest that population size of monophagous butterflies linearly increases with the density of foodplants (KRAUSS *et al.* 2004; BATÁRY *et al.* 2007).

Distribution of eggs showed a slightly different pattern from butterflies, as their presence and number was lower in open patches beside the unpopular poplar patches. This distribution means that butterflies used the food plant patches in open areas, but did not lay many eggs there; different life stages may have different requirements. Eggs were more abundant in hummock and black locust patches where food plants were bigger and food plant number was higher. It seems that the number and size of food plants can jointly explain the egg distribution. Egg distribution could differ from adult distribution in other butterfly species as well, such as *Hypochrysops halietus*, where adult density was high in a track without vegetation, but larvae were present only on the foodplant (DOVER & ROWLINGSON 2005). Other studies showed that adults preferred the habitat suitable for egg laying, so egg density was greater where adults were more abundant, as in

the case of *Aricia artaxerxes* (ELLIS 2003). However, *A. artaxerxes* has a strong attachment to its habitat due to the almost-sessile females and posting males (VARGA, pers. comm.). Our observations on *Z. polyxena* individuals suggest that the activity of this species is influenced by sunlight (KŐRÖSI *et al.*, unpublished data). However, clearings could be too dry for eggs, and drought can be a critical factor in the larval development of butterfly species (SCHWEIGER *et al.* 2006). Clearings were not only dry, but were exposed to nocturnal frost during the egg and early larval stages.

Hummocks and black-locust patches were the best oviposition sites at this disturbed plantation site, an observation confirmed by a latter study (BATÁRY *et al.* 2008), probably due to the large number and size of foodplants. Hummocks are nitrogen-rich and sunny enough to be suitable habitat for the foodplant. Sufficient foodplant is necessary, since excessive egg load can lead to defoliation of the foodplants, as in the case of *Zerynthia cretica*. Egg density depended on foodplant density at this scale; however, in a latter study on egg distribution, we showed that the surrounding foodplant density had no significant effect on egg density at the level of individual food plant shoots (BATÁRY *et al.* 2008).

Larvae showed a different distribution from eggs and butterflies, since they were significantly more abundant in hummock patches. Few larvae were present in black locust and open patches and almost none in poplar patches. Food plant height was highest in hummock and lowest in poplar patches, just like the number of larvae.

Egg distribution changed by the time the development reached larval stage (Table 1 in **Study IV.**). In spite of the large number of eggs in black locust patches (mean 12.7±4.9) eggs per quadrate), larvae number decreased (mean 4.1±1.1 larvae per quadrate). The most probable explanation is that larvae had a higher mortalityrate in black-locust patches. As black locust was growing leaves during the study, transects in black locust became more and more shaded during larval development. Therefore, foodplant patches in black-locust vegetation can be ecological traps. There is also a possibility of larval movement from black locust patches, but it would be also the result of lower habitat quality.

Increasing shade might also lower temperatures and cause either increasing mortality or decreasing growth rate. MEYER and SISK (2001) found that canopy cover is an important factor in the mortality of eggs and larvae, since too much light can dry out eggs, while overshading may be unsuitable for the foodplants. Our results showed that the height of foodplant positively affected both the presence and density of larvae. This finding emphasizes the importance of sufficient foodplant to avoid defoliation and larval starvation (DENNIS 1996).

The most traditional foodplant-based definition of habitat patch would fail in the case of the *Z. polyxena* in this location. Foodplants were available at the study site in large quantity, but the suitability of foodplant patches differed in the four habitat types. The poplar plantation seemed to be a poor habitat for this butterfly; each of the three studied life stages was less numerous there. The butterflies did not use the suitable foodplant patches in

the poplar habitat, which therefore can be regarded as a low-quality habitat or even an ecological trap (ROBERTSON *et al.* 2013), as its quality decreases during the butterfly's development. Defining the habitat based on all the necessary resources (DENNIS *et al.* 2006; VANREUSEL *et al.* 2007) would lead to more precise habitat maps, in contrast to those based merely on foodplant distribution.

Study IV showed the importance of within-patch habitat quality, as the different life stages of the butterfly were revealed to have different habitat requirements, a result that aligns with other studies (THOMAS 1991; ELLIS 2003; DOVER & ROWLINGSON 2005). We point out the importance of within-site variation in habitat quality on the distribution of *Z. polyxena.*

The importance of human-dominated habitats is increasing due to the decline of natural habitats and decrease of natural disturbances (ROBERTSON *et al.* 1995); therefore, the state of these plantation complexes can greatly affect the survival and reproduction of the Southern Festoon and can offer them alternative habitats similar to other insect species that live in riparian forests (ALLEGRO & SCIAKY 2003). Although these human-created plantations are novel ecosystems they can also function as ecological traps for the butterflies (ROBERTSON *et al.* 2013).

SUMMARY

In this study, I discuss three important aspects of butterfly conservation: the significance of ecological studies on butterfly conservation, the importance of habitat use and availability of resources at all life stages for butterflies, and the consequences of the spatial structure of populations. Instead of analysing all of these aspects for one species, I examined three different species: *Maculinea (Phengaris) teleius*, *Coenonympha oedippus* and *Zerynthia polyxena*. All three are protected species, although they are threatened to different degrees. The studies aimed to reveal the points where conservation management can impact the long-term survival of the species. The primary aim, however, was to reveal species' habitat use and requirements in all cases. Knowing the requirements of a species can aid in the creation of suitable habitat management to protect the habitat and the species for survival. As European landscapes are human dominated, butterfly habitats are related to human management. All changes in traditional management, whether increasing or decreasing it, can lead to deterioration of habitats. For this reason, many threatened butterfly species need planned conservation management to ensure their survival.

The current biodiversity crisis appears more critical among butterfly species than other species. The population of specialist butterfly species declined more than generalist species, placing them at even greater risk of extinction. The first step to forming a conservation plan for a species is to locate the populations. Then, it is necessary to survey the population

structure, size and dynamics. Afterwards, the focus turns to the species' habitat requirements and use in order to form a possible management plan for each habitat. Finally, it is necessary to measure the effects of habitat management. In our cases, our initial knowledge of the three species differed between the well-known *M. teleius*, the less-studied *C. oedippus* and the understudied *Z. polyxena*.

The aims of this study were to supplement the existing knowledge about habitat use and population biology in the case of these three species for later conservation management. In the case of *M. teleius,* numerous publications are available dealing with the ecology and conservation of the species; some studies even concentrate on the possible effects of management. Several European research groups have studied the distribution, population size and reproduction biology of *C. oedippus*. In Hungary, the location of one permanent population was known, but population structure, dispersal, habitat use and habitat requirements of the species were unknown. This population of the threatened species was considered to be at high risk for local extinction. *Z. polyxena* ranges in Southern and Eastern Europe. Aside from our study on its egg distribution, there is only one publication about *Z. polyxena,* regarding its population structure and our study on egg distribution. The species is not in immediate danger, but has protected status and may require management actions to preserve its current populations.

The main reasons for butterfly diversity decline in Europe are habitat loss, habitat fragmentation and changes in land. As European landscapes have long been human dominated, many species relying on low-intensity

agricultural use typical of earlier agronomic eras now require conservation-oriented habitat management to be maintained. Agricultural landscapes, especially wet meadows, are affected by intensification or abandonment, both of which can diminish formerly suitable butterfly habitats. Habitat degradation and fragmentation of wet meadows have caused the decline of several butterflies, including *C. oedippus* and *M. teleius*.

M. teleius is an endangered butterfly throughout Europe due to its special life-cycle and habitat loss. Our aims in **Study I** were to describe the microhabitats available for the butterfly in order to determine the factors that influence the presence and density of *M. teleius* as well as to investigate the relationship between host ant species and *M. teleius*. The vicinity of eight fens was chosen for sampling, where four types of microhabitats were available for the butterflies: *Typha-*, *Lythrum-*, *Stachys-*, *Molinia* microhabitat. In five transects around each fen, the number of imagos was counted twice a day during the flight period. The following parameters were measured or assessed along the transects: number of foodplant flowerheads (*Sanguisorba officinalis*), microhabitat type, grazing intensity, soil humidity, vegetation height and host ant presence. The four microhabitat types differed significantly in terms of soil humidity, vegetation height, foodplant density and distance from fen. Generally, *Typha* situated the closest to the fen, had the highest soil humidity and vegetation height; it was followed by *Lythrum-*, *Stachys-* and, *Molinia* microhabitat with decreasing soil humidity and vegetation height. The foodplant with the highest density occurred in the *Lythrum* and *Stachys* microhabitats. Using linear mixed

models, we found that microhabitat type was the most important factor in determining the presence of *M. teleius*. Local grazing intensity had no direct effect on butterflies, while foodplant flowerheads had a positive effect on the abundance of butterflies. The number of butterflies was significantly higher in quadrates where the host ant (*Myrmica scabrinodis*) was present. Our results suggest that the grazing regime should be maintained to support the given distribution of microhabitats and the survival of butterflies.

C. oedippus is one of the most endangered butterflies in Europe due to the decrease in habitats, the current small population size and isolation of most locations. *C. oedippus* occupies wet meadows dominated by Molinietum vegetation. The aim of **Study II** was to estimate some essential parameters of population dynamics (e.g. population size, sex ratio, survival rate, average lifespan) in a single population of *C. oedippus* during a three-year period using a mark–release–recapture method. The population size did not fluctuate during the three years; the total estimated numbers of individuals were 130–270. The survival probability was 0.81–0.84/day in the case of males and 0.70–0.89/day in females. The catchability was between 0.27–0.53 in males and 0.22–0.38 in females. The structure of the population indicates that *C. oedippus* is a sedentary butterfly species, with a low dispersal ability. In the study area, drainage seems to be the main destructive factor for the habitat.

In **Study III**, we enlarged the study area and covered all occupied patches of the habitat complex. The species' presence was recorded in 16 patches, with 12 patches of higher densities. We aimed to gain information

about the population structure, discriminating clusters of habitat patches based on phenology, asynchrony of subpopulations and movement patterns of the species. We also sought to determine whether and how habitat quality affects its population size and density. In each part of the habitat complex, population size and the extent of dispersal among habitats was estimated with a mark–release–recapture method. Effects of habitat quality on daily population size and maximum daily density were also surveyed. The population complex seems viable as the population size was almost 4000 individuals, but divided into 12 subpopulations. Although the layout of the habitat patches suggested the metapopulation approach, the population structure parameters, such as the low dispersal ability of females, did not confirm it. The habitat patches had slightly different quality, causing different population sizes and densities. Three variables stood out from the parameters describing the habitat patches: level of groundwater, height of grass litter and the size of the habitat covered with tussocks. All of these parameters can affect imago or larval survival throughout suitable microclimates. The preferable habitats were covered by large amounts of tussocks, with high grass litter and high but not-too-high level of ground water. Such conditions can be maintained by a light mowing regime and suitable water regulation.

In **Study IV**, we focused on how habitat quality affects the presence and size of butterfly populations and the distribution of different life stages. The aim of **Study IV** was to determine factors affecting the small-scale habitat use of *Z. polyxena*, including the use of foodplant patches by adults and the

distribution of eggs and larvae among foodplant patches; it also sought to reveal the resource requirements of the species at all life stages in a human-dominated landscape. *Z. polyxena* is a vulnerable, but locally abundant species in Hungary. The larva requires birthwort (*Aristolochia clematitis*) as a foodplant. We examined the small-scale habitat use of adults and distribution of eggs and larvae among different vegetation types to reveal the requirements of the species at all life stages. Transect counts were conducted in a tree plantation complex comprised of four types of vegetation. Number (±SE) of adults, eggs and larva were lowest in the poplar plantation (adult 0.3±0.2, egg 1.1±1.1, larva 0.6±0.3). Medium amounts of butterflies were observed in open (adult 8.3±2.9, egg 3.1±2.6, larva 3.1±1.9) and black locust (adult 9.4±4.2, egg 12.7±4.9, larva 4.1±1.1) habitat. The number of butterflies was highest in hummocks (adult 13.5±1.5, egg 12.9±5.7, larva 8.4±2.1). Adults avoided bare ground. We encountered most eggs in dense foodplant patches with high plants. Foodplant height also positively influenced the occurrence of larvae. Although distribution of adults and juvenile forms showed quite similar patterns, we also noted some differences resulting from various environmental conditions in distinct vegetation types. Our study stresses the importance of habitat quality, which affects butterfly population size even in a highly-degraded habitat complex.

ÖSSZEFOGLALÓ

Dolgozatomban az ökológiai kutatások természetvédelmi jelentőségét járom körül, védett nappali lepkék példáján. A lepkék élőhelyhasználata, az egyes fejlődési stádiumok számára szükséges források elérhetősége és a populációk térbeli szerveződése mind jelentősek a természetvédelmi elmélet és gyakorlat szempontjából. Ezeket az aspektusokat három különböző védett nappali lepkefajt modellszervezetként használva vizsgáltam. A vérfű boglárka (*Maculinea (Phengaris) teleius*), az ezüstsávos szénalepke (*Coenonympha oedippus*) és a farkasalma lepke (*Zerynthia polyxena*) védett fajok, habár veszélyeztetettségük mértéke különböző. A vizsgálatok célja volt kideríteni, hogy mely ponton alkalmazhatóak természetvédelmi beavatkozások a fajok hosszútávú túlélésének biztosításához. A legfőbb cél az élőhelyhasználat és a forrásigények feltárása volt mindhárom faj esetében, ezeknek az ismerete ugyanis elengedhetetlenül szükséges a megfelelő természetvédelmi kezelési tervek kidolgozásához. A nappali lepke élőhelyek Európában erőteljes antropogén hatás alatt állnak, a hagyományos kezelés megváltoztatása a területet leromlásához vezethet, akár intenzívebbé válik, akár felhagynak vele. Emiatt sok veszélyeztetett lepkefaj élőhelyének megőrzéséhez szükséges jól megtervezett természetvédelmi beavatkozásokat végezni.

A jelenlegi biodiverzitás krízis erősebben jelentkezik a nappali lepke fajok esetén, mint más csoportoknál. A specialista fajok populációnak

hanyatlása nagyobb mértékű, mint a generalista fajoké, így kihalásuknak nagyobb a veszélye.

A természetvédelmi kezelések kidolgozásához vezető első lépések magukban foglalják a faj populációinak lokalizációját, a populációk méretének, struktúrájának és dinamikájának feltárását. Ezek után lehet a fajok élőhelyhasználatára és forrásszükségletére fókuszálni. A végső cél az ezek alapján felállított kezelési terveknek a megvalósítása és hatásainak ellenőrzése. A kiindulási információk mennyisége különböző a három modellfaj esetén, a *M. teleius* számos kutatás alanya, a *C. oedippus* sokkal kevésbé ismert, míg a *Z. polyxena* kifejezetten ritkán vizsgált.

Kutatásaink célja az volt, hogy kiegészítsék a meglévő ismereteket a három faj élőhely használatáról és populációbiológiájáról a későbbi természetvédelmi intézkedések tudományos megalapozása érdekében.

A *M. teleius* ökológiájával, védelmével és a fajra irányuló természetvédelmi kezelések hatásaival számtalan publikáció foglalkozik.

A *C. oedippus* egy kevésbé vizsgált faj, habár néhány kutatócsoport már tanulmányozta az elterjedését, szaporodásbiológiáját és populációinak méretét. A faj magyarországi elterjedéséről kevés ismeret állt rendelkezésünkre. Egyetlen stabil populáció előfordulása volt ismert, de a populáció szerkezetéről, az egyedek diszperziós képességéről és élőhelyhasználatáról nem voltak adatok. Ráadásul ez a populáció is veszélyeztetetté vált élőhelyének kiszáradása miatt.

A *Z. polyxena* kevéssé tanulmányozott, egyetlen publikáció jelent meg a faj populáció struktúrájáról illetve egy másik a petézési szokásairól. A faj

jelenleg nincs erősen veszélyeztetve, de védett státusa természetvédelmi kezeléseket tehet indokolttá.

A nappali lepke diverzitás csökkenésének fő okai az élőhelyvesztés- és fragmentáció, illetve a gazdálkodás megváltozása. Az európai tájak régóta emberi művelés alatt állnak, ezért sok fajgazdag élőhelytípus erősen függ a hagyományos kis intenzitású mezőgazdasági műveléstől, ennek fenntartása azonban több területen már csak természetvédelmi kezelés formájában lehetséges. Az agrár élőhelyek közül a nedves réteket mind az intenzifikáció, mind a felhagyás veszélyezteti. A nedves rét jellegű élőhelyek leromlása és fragmentációja számos nappali lepke fajt veszélyeztet, köztük a *C. oedippus*-t és a *M. teleius*-t.

A *M. teleius* egész Európában veszélyeztetett, speciális életmódja és élőhelyeinek eltűnése miatt. A dolgozatom alapjául szolgáló I. tanulmány célja a faj számára elérhető potenciális élőhelyfoltok jellemzése volt. Feltételeztük, hogy a *M. teleius* jelenléte és denzitása különbözik a vizsgálati területen megtalálható négy különböző élőhelytípus esetében. Azt vizsgáltuk, hogy a tápnövény mennyisége, a hangyagazda jelenléte és bizonyos környezeti tényezők hogyan befolyásolják a kifejlett egyedek jelenlétét illetve denzitását.

Kunpeszér mellett nyolc, egymáshoz közel eső turján körül jelöltük ki a mintavételi területet. Négy, a faj számára megfelelő élőhelytípus fordult elő: *Typha*-, *Lythrum*-, *Stachys*- és *Molinia* dominálta vegetáció. Öt 50×5 méteres transzektet helyeztünk el minden turjánfolt körül (a turján szélére merőlegesen kifelé), ezek mentén számoltuk az egyedeket naponta kétszer a

repülési időszak alatt. A transzektek mentén a következő paramétereket is feljegyeztük: a tápnövény (*Sanguisorba officinalis*) virágfejeinek száma, élőhelytípus, legelés intenzitása, talajnedvesség, vegetáció magasság, hangyagazda jelenléte. A talajnedvesség, vegetáció magasság, tápnövény denzitás és a turjántól való távolság szignifikánsan különbözött a négy élőhelytípusban. Általában a *Typha* élőhely helyezkedett el legközelebb a turján szegélyéhez, itt volt a legnagyobb a talaj nedvessége és a vegetáció magassága is. Ezen kívül helyezkedett el a *Lythrum* és *Stachys* dominálta élőhely, végül legmesszebb a turjánoktól, az egyre alacsonyabb vegetáció magassággal és talajnedvességgel bíró gyep élőhelytípus. A tápnövény a *Lythrum* és *Stachys* dominálta élőhelytípusban fordult elő a legnagyobb sűrűségben. Lineáris kevert modellek segítségével megállapítottuk, hogy az élőhely típus volt a legfontosabb tényező a *M. teleius* egyedek jelenléte szempontjából. A különböző szintű legelési intenzitásnak nem volt közvetlen hatása a lepkékre, míg a tápnövény virágfejeinek sűrűsége pozitívan befolyásolta a lepkék egyedszámát. Az egyedszám ugyancsak szignifikánsan nagyobb volt azokban a kvadrátokban, ahol a hangyagazda faj (*Myrmica scabrinodis*) jelen volt. Eredményeink szerint a jelenlegi legeltetés megfelelő lehet a faj számára megfelelő élőhelytípusok fenntartása és így a faj túlélésének biztosítása szempontjából.

A *C. oedippus* egyike Európa legveszélyeztetettebb lepkefajainak. Ennek oka élőhelyeinek leromlása és eltűnése, a populációk kis mérete és izoláltsága. A *C. oedippus* Molinietum társulásokban, nedves réteken él. A II. tanulmányban egy Ócsa közeli populáció méretének és

populációdinamikai paramétereinek becslése volt a célunk. A három éves vizsgálat során jelölés-visszafogás módszerrel állapítottuk meg a populáció méretét, ami nem változott jelentős mértékben a vizsgálat időtartama alatt. A teljes becsült egyedszám 130 és 270 között volt. A látszólagos túlélési valószínűség 0,81–0,84/nap volt a hímek és 0,70–0,89/nap a nőstények esetén. A fogási valószínűség 0,27–0,53 között volt a hímek és 0,22–0,38 a nőstények esetén. A populáció szerkezete alapján a *C. oedippus* alacsony diszperziós képességű helytülő faj.

A III. tanulmány elkészítése során kiterjesztettük a vizsgálati területet a környéken talált valamennyi foglalt élőhelyfoltra. A faj 16 élőhelyfoltban volt jelen, ebből 12-ben nagyobb mennyiségben. A populációstruktúra feltárása volt a célunk: a fenológia, aszinkronitás és mozgásmintázat alapján elkülönülő élőhely folt csoportok elkülönítése. Emellett a vizsgálat célja volt, hogy megállapítsuk, hogyan befolyásolja az élőhelyek minősége a szubpopulációk méretét és denzitását. A populációméretet az élőhelykomplexum valamennyi alegységében jelölés-visszafogás módszerrel becsültük, így a foltok közti diszperziós események egy részét is megfigyeltük. Felmértük az élőhely minőségének a populációméretre és denzitásra gyakorolt hatását is.

Az élőhelykomplexum teljes területén közel 4000 egyed volt jelen, ugyanakkor figyelembe kell venni, hogy az egyedek nagy része 12 alpopuláció közt oszlott meg. Az élőhelyfoltok elrendeződése metapopulációs struktúrára utalt, azonban eredményeink szerint ez a metapopuláció nincs egyensúlyi állapotban. A populációstruktúra

55

paraméterei, valamint a nőstények alacsony diszperziós képessége alapján az alpopulációk újratelepülésének valószínűsége alacsony, így a metapopulációkra jellemző gyors kihalás-visszatelepülés dinamika nem működik.

Az élőhelyfoltok minősége eltérő volt, aminek a következtében az alpopulációk mérete és denzitása is különbözött. Ezeket leginkább a talajvízszint, a fűavar magassága és a zsombékokkal fedett terület mérete befolyásolta. Mindhárom paraméter közvetlenül hat a lárvák túlélésére, illetve közvetve az imágók számára szükséges élőhely kialakításában is szerepet játszik. A legkedvezőbb élőhelyeken nagy területeket borít zsombékoló szerkezetű növényzet, nagy mennyiségű fűavar található és a talajvízszint elég magas a Molinietum társulás fenntartásához, viszont elég alacsony a bokrok fejlődéséhez. Ez az élőhely fenntartható rendszeres, de kis intenzitású kaszálással és megfelelő vízvisszatartás szabályzással.

A IV. tanulmány középpontjában az élőhelyminőség populáció méretre gyakorolt hatása állt. A *Z. polyxena* egy védett, de elterjedt és néhol nagy mennyiségben előforduló faj Magyarországon. Hazánkban a lárvák kizárólag farkasalmán (*Aristolochia clematitis*) táplálkoznak. Célunk volt, hogy meghatározzuk a *Z. polyxena* élőhelyhasználatát, figyelembevéve a különböző fejlődési fázisok eltérő élőhelyigényét. Meghatároztuk a tápnövényfoltokban az imágók, a peték és a lárvák eloszlását, miközben feltártuk az egyes fejlődési formák élőhelyigényeit. Transzekt menti számlálással becsültük az egyedek relatív denzitását egy olyan nyárfaültetvényen, ahol négyféle élőhely állt rendelkezésre. Mind a kifejlett

56

egyedek, mind a peték és lárvák száma (±SE) a nyaras területeken volt a legalacsonyabb (lepke 0,3±0,2, pete 1,1±1,1, lárva 0,6±0,3). Valamivel több lepke volt megfigyelhető a nyílt (lepke 8,3±2,9, pete 3,1±2,6, lárva 3,1±1,9) és az akácos (lepke 9,4±4,2, pete 12,7±4,9, lárva 4,1±1,1) élőhelytípusban. Ugyanakkor itt kell megjegyezni, hogy a lárvák száma alacsonyabb volt az akácos foltokban, mint az a lerakott peték száma alapján várható volt. A lepkék legnagyobb számban a zavart domb élőhelyetípusban fordultak elő (lepke 13,5±1,5, pete 12,9±5,7, lárva 8,4±2,1). A kifejlett egyedek elkerülték azokat a területeket, ahol nagy volt a csupasz talajfelület aránya. A legtöbb petét a sűrű és magas tápnövényekkel borított kvadrátokban figyeltük meg. A tápnövények magassága emellett a lárvák mennyiségét is pozitívan befolyásolta. A kifejlett egyedek és a peték, valamint lárvák eloszlása kissé eltért a négy élőhelytípusban, a környezeti paraméterek különbözősége miatt. Vizsgálatunk felhívja a figyelmet az élőhely minőségének egy élőhelyen belüli változatosságának jelentőségére, ami befolyásolja a populációk méretét és eloszlását.

ACKNOWLEDGEMENT

REFERENCES

ALLEGRO, G. & SCIAKY, R. (2003) Assessing the potential role of ground beetles (*Coleoptera, Carabidae*) as bioindicators in poplar stands with a newly proposed ecological index (FAI). *Forest Ecology and Management* **175**: 275–284.

ANTON, C., MUSCHE, M., HULA, V. & SETTELE, J. (2005) Which factors determine the population density of the predatory butterfly *Maculinea nausithous*? In: Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2*. PENSOFT Publishers, Sofia, pp. 57–59.

ARNASON, N. & SCHWARZ, C.J. (1999) Using POPAN-5 to analyse banding data. *Bird Study* **46**: S157-168.

BAGUETTE, M. & SCHTICKZELLE, N. (2003). Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology* **40**: 404–412.

BAGUETTE, M., CLOBERT, J. & SCHTICKZELLE, N. (2011) Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. *Ecography* **34**:170–176.

BÁLINT, Z &, MÁTÉ, A. (2004) Ezüstsávos szénalepke (*Coenonympha oedippus*) fajmegőrzési terv. [False ringlet (*Coenonympha oedippus*) species conservation actionplan.] KvVM Természetvédelmi Hivatala, Budapest

BÁLINT, Z., GUBÁNYI, A. & PITTER, G. (2006) *Magyarország védett pillangóalakú lepkéinek katalógusa a Magyar Természettudományi Múzeum gyűjteménye alapján* [A catalogue of protected papilioformid butterflies of Hungary based on the collection of the Hungarian Natural History Museum]. Magyar Természettudományi Múzeum, Budapest, 136 pp.

BARTOŠ, M., JANEČEK, S. & KLIMEŠOVÁ, A (2011) Effect of mowing and fertilization on biomass and carbohydrate reserves of *Molinia caerulea* at two organizational levels. *Acta Oecologica* **37**:299–306.

BATÁRY, P., ÖRVÖSSY, N., KŐRÖSI, Á. & PEREGOVITS, L. (2008) Egg distribution of the southern festoon (*Zerynthia polyxena*). *Acta Zoologica Academiae Scientiarum Hungaricae* **54**(4):401–410.

BATÁRY, P., ÖRVÖSSY, N., KŐRÖSI, Á., VÁLYI-NAGY, M. & PEREGOVITS, L. (2007) Microhabitat preferences of *Maculinea teleius* (Lepidoptera: Lycaenidae) in a mosaic landscape. *European Journal of. Entomology* **104**:731–736.

BERGMAN, K.O. & LANDIN, J. (2002) Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation* **108**: 361–369.

BERGMAN, K.O., ASKLING, J., EKBERG, O., IGNELL, H., WAHLMAN, H. & MILBERG, P. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography* **27**:619–628.

BONELLI, S., CANTERINO, S. & BALLETTO, E. (2010) Ecology of *Coenonympha oedippus* (Fabricius, 1787) (Lepidoptera: Nymphalidae) in Italy. *Oedippus* **26**:25–30.

BONELLI, S., CROCETTA, A., BARBERO, F. & BALLETTO, E. (2005) Oviposition behaviour in the myrmecophilous butterfly *Maculinea alcon* (Lepidoptera: Lycenidae). In: SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2.* PENSOFT Publishers, Sofia, pp. 65–68.

BOURN, N.A.D., PEARMAN, G.S, GOODGER, B., THOMAS, J.A. & WARREN, M.S. (2000) Changes in the status of two endangered butterflies over two decades and the influence of grazing management. In: ROOK, A. J. & PENNING, P. D. (eds) *Grazing management.* British Grassland Society, Reading, pp 141–146.

BOZANO, G.C. (2002) Guide to the butterflies of the Palearctic region. Satyrinae part III. Omnes Artes, Milano

BRAKEFIELD, P.M. (1982) Ecological studies on the butterfly *Maniola jurtina* in Britain. II. Population dynamics: the present position. *Journal of Animal Ecology* **51**:99–144.

BRÄU, M., DOLEK, M. & STETTMER, C. (2010) Habitat requirements, larval development and food preferences of the German population of the

False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) – research on the ecological needs to develop management tools. *Oedippus* **26**:41–51.

BURNHAM, K.P. & ANDERSON, D.R. (2002) Model selection and multi-model inference. A practical information-theoretic approach. 2nd ed. Springer-Verlag, New York

ČELIK, T. & VEROVNIK, R. (2010) *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Slovenia. *Oedippus* **26**:7–15.

ČELIK, T. (2004) Population dynamics of endangered species *Coenonympha oedippus* Fabricius, 1787 (Lepidoptera:Satyridae) on the Ljubljansko Baarje (Slovenia). *Acta Entomologica Slovenica* **12**:99–114.

ČELIK, T. (2012) Adult demography, spatial distribution and movements of *Zerynthia polyxena* (Lepidoptera: Papilionidae) in a dense network of permanent habitats. *European Journal of Entomology.* **109**: 217–227.

ČELIK, T., VREŠ, B. & SELIŠKAR A. (2009) Determinants of within-patch microdistribution and movements of endangered butterfly *Coenonympha oedippus* (Fabricius, 1787) (Nymphalidae: Satyrinae). *Hacquetia* **8**:115–128.

CIZEK, O., ZAMECNIK, J., TROPEK, R.., KOCAREK, P. & KONVICKA, M (2012) Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation* **16**(2):215–226.

COOK, L.M., BROWER, L.P. & CROZE, H.J. (1967) The accuracy of a population estimation from multiple recapture data. *Journal of Animal Ecology* 6: 57-60.

CROXTON, P.J., HANN, J.P., GREATOREX-DAVIES, J.N. & SPARKS, T.H. (2005) Linear hotspots? The floral and butterfly diversity of green lanes. *Biological Conservation* **121**:579–584.

DAPPORTO, L.& DENNIS, R.L.H. (2013) The generalist-specialist continuum: testing predictions for distribution and trends in British butterflies. *Biological Conservation* **157**:229–236.

DENNIS, R.L.H. (1996) Oviposition in *Zerynthia cretica* (Rebel, 1904): loading on leaves, shoots and plant patches (Lepidoptera, Papilionidae). *Nota Lepidopterologica* **18**:3–15.

DENNIS, R.L.H., SHREEVE, T. & VAN DYCK, H. (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity Conservation* **15**:1943-1966.

DENNIS, S. & VAN DYCK, H. (2003) Towards a resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* **102**:417–426.

DIERKS, A. & FISCHER, K. (2009) Habitat requirements and niche selection of *Maculinea nausithous* and *M. teleius* (Lepidoptera: Lycaenidae) within a large sympatric metapopulation. *Biodiversity and Conservation* **18**(13): 3663–3676.

DOLEK, M, STETTMER, C., BRÄU, M. & SETTELE, J. (2010) Oedippus in *Oedippus*. 01

DOVER, J. & SETTELE, J. (2009) The influence of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation* **13**:3–27.

DOVER, J.W. & ROWLINGSON, B. (2005) The western jewel butterfly (*Hypochrysoops halietus*): factors affecting adult butterfly distribution within native Banksia bushland in an urban setting. *Biological Conservation* **122**: 599–609.

DOVER, J.W., SPENCER, S., COLLINS, S., HADJIGEORGIOU, I. & RESCIA, A. (2011) Grassland butterflies and low intensity farming in Europe. *Journal of Insect Conservation* **15**:129–137.

EKROOS, J., HELIOLA, J. & KUUSSAARI, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology* **47**:459–467.

ELLIS, S. (2003) Habitat quality and management for the northern brown argus butterfly *Aricia artaxerxes* (Lepidoptera: Lycaenidae) in North East England. *Biological Conservation* **113**: 285–294.

ERHARDT, A. & THOMAS, J.A. (1991) Lepidoptera as indicators of change in the seminatural grasslands of lowland and upland Europe. In: COLLINS, N.M. & THOMAS, J.A. (eds) *The conservation of insects and their habitats.* Academic Press, London pp 213–237.

FIGURNY E. & WOYCIECHOWSKI M. (1998) Flowerhead selection for oviposition by females of the sympatric butterfly species *Maculinea*

teleius and *M. nausithous* (Lepidoptera: Lycenidae). *Entomol. Gener.* **23**: 215–222.

Filz, K.J., Wiemers, M., Herrig, A., Weitzel, M. & Schmitt , T. (2014) A question of adaptability - Climate and habitat change lower trait diversity in butterfly communities in south-western Germany. *European Journal of Entomology* **110**(4):633–642.

Fischer, K. (1998) Population structure, mobility and habitat selection of the butterfly *Lycaena hippothoe* (Lycaenidae: Lycaenini) in eastern Germany. *Nota Lepidopterologica* **21**: 14–30.

Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C. L. & Murphy, D. (2002) Assessing the roles of patch quality, area and isolation in predicting metapopulation dynamics. *Conservation Biology* **16**: 706–716.

Fleishman, E.D., Murphy, D. & Brussard. P.F. (2000) A new method for selection of umbrella species for conservation planning. *Ecological Applications* **10**:569-579.

Franzén, M.; Nilsson, S.G.; Johansson, V. & Ranius, T. (2013) Population Fluctuations and Synchrony of Grassland Butterflies in Relation to Species Traits. PLoS ONE 8(10): e78233.

Fred, S.M., O'Hara, R.B. & Brommer, J.E. (2006) Consequences of the spatial configuration of resources for the distribution and dynamics of the endangered *Parnassius apollo* butterfly. *Biological Conservation* **130**: 183–192.

Giraudoux, P. (2014) Package 'pgirmess', url: http:// perso.orange.fr/giraudoux

Glinka U. & Settele J. (2005) The effect of ant communities and spatial pattern for *Maculinea nausithous*. In: Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2.* PENSOFT Publishers, Sofia, p. 72.

Griebeler E.M. & Seitz A. (2002) An individual based model for the conservation of the endangered Large Blue Butterfly, *Maculinea arion* (Lepidoptera: Lycaenidae). *Ecological Modelling.* **156**: 43–60.

GRUNDEL, R., PAVLOVIC, N.B. & SULZMAN C.L. (1998) Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. *Biological Conservation* **85**: 47–53.

Habitat Directive (1979) (Council of Europe Convention on the Conservation of European Wildlife and Natural Habitats; URL: http://conventions.coe.int/treaty/en/Treaties/Html/104.htm)

HALADA, L., EVANS, D., ROMÃO, C. & PETERSEN, J. (2011) Which habitats of European importance depend on agricultural practices*? Biodiversity Conservation* **20**:2365–2378.

HAMBLER, C., HENDERSON, P.A. & SPEIGHT, M.A. (2011) Extinction rates, extinction-prone habitats, and indicator groups in Britain and at larger scales. *Biological Conservation* **144**:713–721.

HANSKI, I. & GLIPIN, M.E. (1997) *Metapopulation biology. Ecology, genetics and evolution.* Academic Press, San Diego

HANSKI, I. & SIMBERLOFF, D. (1997) *The metapopulation approach, its history, conceptual domain, and application to conservation.* pp. 5–26. In: HANSKI, I. & GILPIN, M.E. (eds.), Metapopulation Biology. Academic Press, San Diego, California.

HANSKI, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* **42**:7–38.

HANSKI, I. (1998) Metapopulation dynamics. *Nature* **396**:41–49.

HANSKI, I. (1999) *Metapopulation ecology.* Oxford University Press, Oxford

HANSKI, I. (2003) Biology of extinctions in butterfly metapopulations. In: BOGGS, C. L., WATT, W. B. & EHRLICH, P. R. (eds) *Butterflies: Ecology and Evolution Taking Flight.* University of Chicago Press, Chicago, pp 577–602

HANSKI, I., ALHO, J. & MOILANEN, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**:239–251.

HANSKI, I., KUUSSAARI, M. & NIEMINEN, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* **75**: 747–762.

HANSKI, I., MOILANEN, A., PAKKALA, T. & KUUSSAARI, M. (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* **10**: 578–590.

HASSAN, R., SCHOLES, R. & ASH, N. (2005) Millenium Ecosystem Assessment *Ecosystems and Human Well-being: Current State and Trends*, Volume 1 pp. 838.

HOTHORN, T., HORNIK, K. & ZEILEIS, A. (2006) Unbiased Recursive Partitioning: A Conditional Inference Framework. *Journal of Computational and Graphical Statistics* **15**: 651-674.

HOVESTADT, T., BINZENHOFER, B., NOWICKI, P. & SETTELE, J. (2011) Do all inter-patch movements represent dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. *Journal of Animal Ecology* **80**:1070–1077.

IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Accessed 15 November 2011

JOHST, K., DRECHSLER, M., THOMAS, J. & SETTELE, J. (2006) Influencing of mowing on the persistence of two large blue butterfly species. *Journal of Applied Ecology* **43**:333–342.

JOY, J. & PULLIN, A.S. (1996) The effects of flooding on the survival and behaviour of overwintering large heath butterfly *Coenonympha tullia* larvae. *Biological Conservation* **82**:61–66.

KÉRY, M., MATTHIES, D. & FISCHER, M. (2001) The effect of plant population size on the interactions between the rare plant *Gentiana cruciata* and its specialized herbivore *Maculinea rebeli*. *Journal of Ecology* **89**: 418–427.

KLEIJN, D., KOHLER, F., BÁLDI, A., BATÁRY, P., CONCEPCION, E.D., CLOUGH, Y., DIAZ, M., GABRIEL, D., HOLZSCHUH, A., KNOP, E., KOVÁCS, A., MARSHALL, E.J.P., TSCHARNTKE, T. & VERHULST, J. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B* **276**:903–909.

KONVIČKA, M., HULA, V. & FRIC, Z. (2003) Habitat of pre-hibernating larvae of endangered butterfly *Euphydryas aurinia* (Lepidoptera:

Nymphalidae): What can be learned from habitat composition and architecture. *European Journal of Entomology* **100**: 313–322.

KŐRÖSI, Á., ÖRVÖSSY, N., BATÁRY, P., HARNOS, A. & PEREGOVITS, L. (2012) Different habitat selection by two sympatric *Maculinea* butterflies at small spatial scale. *Insect Conservation and Diversity* **5**(2): 118–126

KŐRÖSI, Á., ÖRVÖSSY, N., BATÁRY, P., KÖVÉR, S. & PEREGOVITS, L. (2007) Restricted within-habitat movement and time-constrained egg-laying of female *Maculinea rebeli* butterflies. *Oecologica* **156** (2): 455–464.

KŐRÖSI, Á., SZENTIRMAI, I., BATÁRY, P., KÖVÉR, S., ÖRVÖSSY, N. & PEREGOVITS, L. (2014) Effects of timing and frequency of mowing on the threatened scarce large blue butterfly – A fine-scale experiment. *Agriculture Ecosystems & Environment* **196**:24–33.

KRAUSS, J., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J*ournal of Biogeography* **30**:889–900.

KRAUSS, J., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2004) Landscape occupancy and local population size depends on food-plant distribution in the butterfly *Cupido minimus*. *Biological Conservation* **120**: 355–361.

KRUESS, A. & TSCHARNTKE, T. (2002) Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps. Conservation Biology **16** (6): 1570–1580

KUDRNA, O. (2002) The distribution atlas of European butterflies. *Oedippus* **20**:1–343.

KÜHN, E., FELDMANN, R., THOMAS, J. & SETTELE, J. (2005) *Ecology and Conservation of Butterflies in Europe. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 1.* PENSOFT Publishers, Sofia, 128. pp.

LEBRETON, J-D., BURNHAM, K.P., CLOBERT, J. & ANDERSON, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monography* **62**:67–118

LENDA, M. & SKÓRKA, P. (2010) Patch occupancy, number of individuals and population density of the Marbled White in a changing agricultural landscape. *Acta Oecologica* **36**:497–506.

LHONORE, J. & LAGARDE, M. (1999) Biogeography, ecology and conservation of *Coenonympha oedippus* (Fab., 1787) (Lepidoptera : Nymphalidae : Satyrinae) *Annales de la Societe Entomologique de France* **S35**:299–307.

MAES, D. & VAN DYCK, H. (2001) Butterfly diversity loss of Flanders (North Belgium): Europe's worst case scenario? *Biological Conservation* **99**: 263-276.

MAES, D., VANREUSEL, W., TALLOEN, W., VAN DYCK, H. (2004) Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae) *Biological Conservation* **120**: 229-241.

MEYER, C.L. & SISK, T.D. (2001) Butterfly response to microclimatic conditions following ponderosa pine restoration. *Restoration Ecology* **9**: 453–461.

MOLNÁR, Z., BÍRÓ, M., BÖLÖNI, J. & HORVÁTH, F. (2008) Distribution of the (semi)-natural habitats in Hungary I. – Marshes and grasslands. *Acta Botanica Hungarica* **50**: 59–105.

MOROŃ, D., LENDA, M., SKÓRKA, P., SZENTGYÖRGYI, H., SETTELE, J. & WOYCIECHOWSKI, M. (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation* **142**: 1322-1332.

MUNGUIRA, M.L., MARTIN, J., GARCIA-BARROS, E. & VIEJO, J.L. (1997) Use of space and resources in a Mediterranean population of the butterfly *Euphydryas aurinia*. *Acta Oecologica* **18**: 597–612.

MUSCHE, M., ANTON, C., WORGAN, A. & SETTELE, J. (2005) Do ant cues influence the oviposition preference in the myrmecophilous *Maculinea nausithous*? In: SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2.* PENSOFT Publishers, Sofia, pp. 80–81.

NOWICKI, P., PĘPKOWSKA, A., KUDŁEK, J., SKÓRKA, P., WITEK, M. & WOYCIECHOWSKI, M. 2005a. Landscape scale research in butterfly population ecology – *Maculinea* case study. In: SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2.* PENSOFT Publishers, Sofia, pp. 140–143.

NOWICKI, P., PEPKOWSKA, A., KUDLEK, J., SKÓRKA, P., WITEK, M., SETTELE, J. & WOYCIECHOWSKI, M. (2007) From metapopulation theory to conservation recommendations: Lessons from spatial occurrence and abundance patterns of Maculinea butterflies. *Biological Conservation* **140**: 119–129.

NOWICKI, P., VRABEC, V., BINZENHÖFER, B., FEIL, J., ZAKŠEK, B., HOVESTADT, T. & SETTELE, J. (2014) Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance *Landscape Ecology* **29**:401–412.

NOWICKI, P., WITEK, M., SKÓRKA, P., SETTELE, J. & WOYCIECHOWSKI, M. (2005b) Population ecology of the endangered butterflies *Maculinea teleius* and *M. nausithous* and the implications for conservation. *Popul. Ecol.* **47**: 193–202.

OOSTERMEIJER, J.G.B. & VAN SWAAY, C.A.M. (1998) The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biological Conservation* B:271–280.

ÖCKINGER, E. & SMITH, H.G. (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* **149**:526–534.

ÖCKINGER, E. (2006) Possible metapopulation structure of the threatened butterfly *Pyrgus armoricanus* in Sweden. *Journal of Insect Conservation* **10**:43–51.

ÖCKINGER, E., BERGMAN, K.O., FRANZEN, M., KADLEC, T., KRAUSS, J., KUUSSAARI, M., PÖYRY, J., SMITH, H.G., STEFFAN-DEWENTER, I. & BOMMARCO, R. (2012) The landscape matrix modifies the effect of

habitat fragmentation in grassland butterflies. *Landscape Ecology* **27**:121–131.

ÖRVÖSSY, N., VOZÁR, Á., KŐRÖSI, Á., BATÁRY, P. & PEREGOVITS, L. (2010) Structure and size of a threatened population of the False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Hungary. *Oedippus* **26**:31–37.

PARMESAN, C. (2003) Butterflies as bioindicators for climate change effects. In: BOGGS, C.L., WATT, W.B. & EHRLICH, P.R. (eds) Butterflies: Ecology and Evolution Taking Flight. University of Chicago Press, Chicago, pp 541–560.

PECSENYE, K., BERECZKI, J., TIHANYI, B., TÓTH, A., PEREGOVITS, L. & VARGA, Z. (2007) Genetic differentiation among the *Maculinea* species (Lepidoptera: Lycaenidae) in eastern Central Europe. *Biological Journal of the Linnean Society* **91**(1):11–21.

PEREIRA, H.M., FERRIER, S., WALTERS, M., GELLER, G.N. *et al.* (2013) Essential Biodiversity Variables. *Science* **339**: 277–278.

PULLIN, A.S. (2002) *Conservation biology.* Cambridge University Press, Cambridge, UK. pp. 345.

R Development Core Team (2004, 2011) R: *A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/

RABASA, S.G., GUTIÉRREZ, D. & ESCUDERO, A. (2008) Relative importance of host plant patch geometry and habitat quality on the patterns of occupancy, extinction and density of the monophagous butterfly *Iolana iolas*. *Oecologia* **156**:491–503.

ROBERTSON, B.A., REHAGE, J.S. & SIH, A. (2013) Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution* **28**: 552–560.

ROBERTSON, P.P.A., CLARKE, S.A. & WARREN, M.S. (1995) Woodland management and butterfly diversity. Pp. 111–122. *In:* PULLIN, A. S. (ed.): *Ecology and conservation of butterflies.* Chapman and Hall, London.

SAMWAYS, M.J., BAZELET, C.S. & PRYKE, J.S. (2010) Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation* **19**:2949–2962.

SANFORD, M.P.; DENNIS, D.M. & BRUSSARD, P.F. (2011) Distinguishing habitat types and the relative influences of environmental factors on patch occupancy for a butterfly metapopulation. *Journal of Insect Conservation* **15**:775–785.

ŠAŠIĆ, M. (2010) False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Croatia: current status, population dynamics and conservation management. *Oedippus* **26**:16–19.

SAWCHIK, J., DUFRÊNE, M., & LEBRUN, P. (2003) Estimation of habitat quality based on plant community, and effects of isolation in a network of butterfly habitat patches. *Acta Oecologica* **24**:25–33.

SCHTICKZELLE, N., CHOUTT, J., GOFFART, P., FICHEFET, V. & BAGUETTE, M. (2005) Metapopulation dynamics and conservation of the marsh fritillary butterfly: Population viability analysis and management options for a critically endangered species in Western Europe. *Biological Conservation* **126**: 569–581.

SCHTICKZELLE, N., MENNECHEZ, G. & BAGUETTE, M., (2006) Dispersal depression with habitat fragmentation in the bog fritillary. *Ecology* **87**: 1057–1065.

SCHWEIGER, O., DORMANN, C.F., BAILEY, D. & FRENZEL, M. (2006) Occurrence pattern of *Pararge aegeria* (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure. *Landscape Ecology* **211**: 989–1001.

SEITZ, A. (1906) *The Macrolepidoptera of the Palearctic Region 1*, Stuttgart pp. 379.

SETTELE, J., KÜHN, E. & THOMAS, J.A. (2005) *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2.* PENSOFT Publishers, Sofia, 289. pp.

SHREEVE, T.G. & DENNIS, R.L.H. (2011) Landscape scale conservation: resources, behaviour, the matrix and opportunities. *Journal of Insect Conservation* **15**:179–188.

SIMBERLOFF, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* **83**:247-257.

SKÓRKA, P. & LENDA, M., (2010) Abandoned fields as refuges for butterflies in agricultural landscapes of Eastern Europe. In: Harris, E.L., Harris, E.L., Davies, N.E., Davies, N. E. (Eds.), *Insect Habitats: Characteristics, Diversity and Management.* Nova Science Publishers, New York, pp. 83–103.

SKÓRKA, P., SETTELE, J. & WOYCIECHOWSKI, M. (2007) Effects of management cessation on grassland butterflies in southern Poland. *Agriculture, Ecosystems & Environment* 121: (4) 319-324.

SLANCAROVA, J., BENES, J., KRISTYNEK, M., KEPKA, P. & KONVIČKA, M. (2013) Does the surrounding landscape heterogeneity affect the butterflies of insular grassland reserves? A contrast between composition and configuration. *Journal of Insect Conservation* **18**:1–12.

SMALLIDGE, P.J. & DONALD, J.L. (1997) Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. *Landscape and Urban Planning* **38**: 259–280.

SPITZER, L., BENES, J., DANDOVA, J., JASKOVA, V. & KONVICKA, M., (2009) The Large Blue butterfly, *Phengaris [Maculinea] arion*, as a conservation umbrella on a landscape scale: The case of the Czech Carpathians. *Ecological Indicators* **9**:1056–1063

STASINOPOULOS, M., RIGBY, B. & AKANTZILIOTOU, C. (2012) Instructions on how to use the gamlsss package in R. http://www.gamlss.org/images/stories/papers/gamlss-manual.pdf. Accessed 03 August 2012

STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2000) Butterfly community structure in fragmented habitats. *Ecological Letters* **3**:449–456.

STOATE, C., BÁLDI, A., BEJA, P., BOATMAN, N.D., HERZON, I., VAN DOORN, A., DE SNOO, G.R., RAKOSY, L. & RAMWELL, C. (2009) Ecological impacts of early 21st century agricultural change in Europe—a review. *Journal of Environmental Management* **91**:22–46.

STRIJKER, D. (2005) Marginal lands in Europe—causes of decline. *Basic and Applied Ecology* **6**: (2) 99-106.

SUTCLIFFE, O.L., THOMAS, C.D., YATES, T.J. & GREATOREX-DAVIES, J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia* 109:235–241

TARTALLY, A. & CSŐSZ, S. (2004) Data on the ant hosts of the *Maculinea* butterflies (Lepidoptera: Lycenidae) of Hungary. *Termvéd. Közl.* **11**: 309–317. (in Hungarian, with English summary).

TARTALLY, A. (2008) Host ant use of Maculinea teleius in the Carpathian Basin (Lepidoptera: Lycaenidae) *Acta zoologica Academiae Scientiarum Hungaricae* **54**:257–268.

THOMAS, C.D. & HANSKI, I. (1997) Butterfly metapopulations. Pp. 359–386. *In:* HANSKI, I. & GILPIN, M. E. (eds): *Metapopulation biology, ecology, genetics and evolution.* Academic Press, San Diego.

THOMAS, C.D., SINGER, M.C. & BOUGHTON, D.A. (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist* **148**: 957–975.

THOMAS, C.D., THOMAS, J.A. & WARREN, M.S. (1992) Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**: 563–567.

THOMAS, J.A. & ELMES, G.W. (2001) Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. *Proc. R. Soc. Lond. B.* **268**: 471–477.

THOMAS, J.A. (1984) The Behaviour and Habitat Requirement of *Maculinea nausithous* (the Dusky Large Blue Butterfly) and *M. teleius* (the Scarce Large Blue) in France *Biological Conservation.* **28**: 325–347.

THOMAS, J.A. (1991) Rare species conservation: case studies of European butterflies. In: SPELLERBERG, I., GOLDSMITH, B. & MORRIS, M. G.

(eds.) *The scientific management of temperate communities for conservation.* Blackwell, Oxford, pp 149–197.

THOMAS, J.A. (1994) The ecology and conservation of *Maculinea arion* and other European species of large blue. In: Pullin A. (ed): *Ecology and conservation of butterflies.* Chapman & Hall, London, pp. 180–196.

THOMAS, J.A., (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**: 339–357.

THOMAS, J.A., BOURN, N.A.D., CLARKE, R.T., STEWART, K.E., SIMCOX, D.J., PEARMAN, G.S., CURTIS, R. & GOODGER, B. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B* **268**:1791–1796.

THOMAS, J.A., CLARKE, R.T., ELMES, G.W. & HOCHBERG, M.E. (1998) Population dynamics in the genus *Maculinea* (Lepidoptera: Lycenidae). In: Dempster J.P. & McLean I.F.G. (eds): *Insect populations*. Chapman & Hall, London, pp. 261–290.

THOMAS, J.A., CLARKE, R.T., RANDLE, Z., SIMCOX, D. J., SCHÖNROGGE, K., ELMES, G.W., WARDLAW, J.C. & SETTELE, J. (2005) Maculinea and myrmecophiles as sensitive indicators of grassland butterflies (umbrella species), ants (keystone species) and other invertebrates. *In:* SETTELE, J., KÜHN, E. AND THOMAS, J.A., eds. *Studies on the Ecology and Conservation of Butterflies in Europe.* Sofia, Bulgaria: Pensoft, pp. 28-31.

THOMAS, J.A., ELMES, G.W., WARDLAW, J.C. & WOYCIECHOWSKI, M. (1989) Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* **79**: 452–457.

THOMAS, J.A., SIMCOX, D.J. & HOVESTADT, T., (2011) Evidence based conservation of butterflies. *Journal of Insect Conservation* **15**: 241–258.

THOMAS, J.A., SIMCOX, D.J., WARDLAW, J.C., ELMES, G.W., HOCJBERG, M. & CLARKE, R.T. (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *Journal of Insect Conservation* **2**: 39–46.

73

THOMAS, J.A., TELFER, M.G., ROY, D.B., PRESTON, C.D., GREENWOOD, J.J.D., ASHER, J., FOX, R., CLARKE, R.T. & LAWTON, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303, 1879–1881.

TSCHARNTKE, T., STEFFAN-DEWENTER, I., KRUESS, A. & THIES, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* **12**:354–363.

TURLURE, C., CHOUTTE, J., VAN DYCK, H., BAGUETTE, M. & SCHTICKZELLE, N. (2010) Functional habitat area as a reliable proxy for population size: case study using two butterfly species of conservation concern. *Journal of Insect Conservation* **14**:379–388.

VAN DYCK, H., OOSTERMEIER, J.G.B., TALLOEN, W., FEENSTRA, V. & VAN DER HIDDE, A. & WYNHOFF, I. (2000) Does the presence of ant nests matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proc. R. Soc. Lond. B.* **267**: 861–866.

VAN HALDER, I., BARBARO, L., CORCKET, E. & JACTEL, H. (2008) Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations *Biodiversity and Conservation* **17**:1149–1169

VAN STRIEN, A.J., VAN DUUREN, J., FOPPEN, R.P.B. & SOLDAAT, L.L. (2009) A typology of indicators of biodiversity change as a tool to make better indicators. *Ecologycal Indicators* **9***:* 1041–1048.

VAN STRIEN, A.J., VAN SWAAY, C.A.M. & KÉRY, M. (2011) Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in the Netherlands. *Ecological Applications* **21**(7) 2510–2520.

VAN SWAAY, C. A. M. (2014) Tracking butterflies for effective conservation. Thesis, Wageningen University pp. 219.

VAN SWAAY, C., WYNHOFF, I., VEROVNIK, R., WIEMERS, M., LÓPEZ MUNGUIRA, M., MAES, D., SASIC, M., VERSTRAEL, T., WARREN, M. & SETTELE, J. (2010b) *Zerynthia polyxena*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org> Downloaded on 28 September 2014.

VAN SWAAY, C.A.M. & WARREN, M.S. (1999) *Red Data Book of European Butterflies (Rhopalocera).* Nature and Environment Series No. 99. Council of Europe, Strasbourg, 260 pp.

VAN SWAAY, C.A.M. & WARREN, M.S. (2003) *Prime Butterfly Areas in Europe: Priority sites for conservation.* National Reference Centre for Agriculture, Nature and Fisheries, Ministry of Agriculture, Nature Management and Fisheries, The Netherlands.

VAN SWAAY, C.A.M. (1990) An assessment of the changes in butterfly abundance in the Netherlands during the 20th Century. *Biological Conservation,* **52**:287–302.

VAN SWAAY, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation* **104**:315–318.

VAN SWAAY, C.A.M. (2013) The European Grassland Butterfly Indicator: 1990–2011. Technical Report. European Environment Agency, Luxembourg.

VAN SWAAY, C.A.M., COLLINS, S., DUŠEJ, G., MAES, D., MUNGUIRA, M.L., RAKOSY, L., RYRHOLM, N., ŠAŠIĆ, M., SETTELE, J., THOMAS, J.A., VEROVNIK, R., VERSTRAEL, T., WARREN, M., WIEMERS, M. & WYNHOFF, I. (2012) Dos and Don'ts for butterflies of the Habitats Directive of the European Union. *Nature Conservation* **1**:73–153.

VAN SWAAY, C.A.M., CUTTELOD, A., COLLINS, S., MAES, D., LÓPEZ, MUNGUIRA, M., ŠAŠIĆ, M., SETTELE, J., VEROVNIK, R., VERSTRAEL, T., WARREN, M., WIEMERS, M. & WYNHOFF, I. (2010a) European red list of butterflies. Luxembourg: Publications Office of the European Union

VAN SWAAY, C.A.M., NOWICKI, P., SETTELE, J. & VAN STRIEN, A.J., (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* **17**(14): 3455–3469.

VAN SWAAY, C.A.M., WARREN, M. & LOÏS, G. (2006) Biotope use and trends of European butterflies. *Journal of Insect Conservation* **10** (2): 189–209.

VANREUSEL, W. & VAN DYCK, H. (2007) When functional habitat does not match vegetation types: A resource-based approach to map butterfly habitat. *Biological Conservation* **135**: 202–211.

75

WAHLBERG, N., KLEMETTI, T. & HANSKI, I. (2002) Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography* **25**: 224–232.

WALKER, M.P., DOVER, J.W., SPARKS, T.H. & HINSLEY, S.A. (2006) Hedges and green lanes: vegetation composition and structure. *Biodiversity and Conservation* **15**:2595–2610.

WALLIS DE VRIES, M. F. (2004) A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. *Conserv. Biol.* **18**: 489–499.

WARREN, M. S., HILL, J. K. & THOMAS, J. A., *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**:65–69.

WEIBULL, A.C. & OSTMAN, O. (2003) Species composition in agroecosystems: the effect of landscape, habitat, and farm management. *Basic and Applied Ecology* **4**:349–361.

WHITE, G.C. & BURNHAM, K. (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**: 120–138.

ZIMMERMANN, K., FRIC, Z., FILIPOVÁ, L. & KONVIČKA, M. (2005) Adult demography, dispersal and behaviour of *Brenthis ino* (Lepidoptera: Nymphalidae): how to be a successful wetland butterfly. *European Journal of Entomology.* **102**: 699–706.

APPENDIX

Microhabitat preferences of *Maculinea teleius* (Lepidoptera: Lycaenidae) in a mosaic landscape

PÉTER BATÁRY*, NOÉMI ÖRVÖSSY*, ÁDÁM KŐRÖSI, MARIANNA VÁLYI NAGY and LÁSZLÓ PEREGOVITS

Hungarian Natural History Museum, Ludovika tér 2., H-1083 Budapest, Hungary; e-mail: batary@nhmus.hu

Abstract. The Scarce Large Blue (*Maculinea teleius*) is an endangered butterfly throughout Europe due to its special life-cycle and habitat loss. Our aims were to describe the microhabitats available to this butterfly, to test what factors influence the presence and density of *M. teleius* adults and to investigate the relationship between host ant species and *M. teleius*. The vicinities of eight fens were sampled, where there are four types of microhabitats available for this butterfly: Narrowleaf Cattail (*Typha angustifolia*), Purple Loosestrife (*Lythrum salicaria*), Marsh Woundwort (*Stachys palustris*) and Purple Moorgrass (*Molinia coerulea*) dominated vegetation. In five transects (50 × 5 m) around each fen (running from the edge of the fen into the meadows) the number of imagos was counted twice a day during the flight period. Along the transects, the following parameters were measured or assessed: number of flowerheads of foodplant (*Sanguisorba officinalis*), microhabitat type, grazing intensity, soil humidity, vegetation height and host ant presence. The four microhabitat types differed significantly in soil humidity, vegetation height, foodplant density and distance from a fen. Generally the Typha microhabitat, situated closest to fens, had the highest soil humidity and vegetation height, followed by the Lythrum, Stachys and finally the Molinia microhabitat along a gradient decreasing soil humidity and vegetation height. The foodplant was most abundant in the Lythrum and Stachys microhabitats. Using linear mixed models and forward stepwise manual selection we found that microhabitat type was the most important factor determining the presence of *M. teleius*. The local grazing intensity had no direct effect but flowerheads of the foodplant had a positive effect on the abundance of butterflies. The number of butterflies was significantly higher in quadrats where the host ant (*Myrmica scabrinodis*) was present compared to those where they were absent. Our results suggest that grazing should be continued in order to maintain the current distribution of microhabitats and survival of the butterflies.

INTRODUCTION

Wet meadows are among the most important habitats of threatened butterflies in Europe (Kühn et al., 2005). More than half of the Hungarian Prime Butterfly Areas (PBA) are wet meadows (Van Swaay & Warren, 2003). It is now widely demonstrated that agricultural intensification (e.g. intense grazing, land drainage or improvement of grasslands) reduces the diversity and abundance of butterflies associated with extensively managed wet meadows (e.g. Van Swaay & Warren, 1999; Konvička et al., 2003; Zimmermann et al., 2005). Furthermore, as a result of changes in human land-use, the extensively managed semi-natural meadows have become increasingly fragmented (Kéry et al., 2001). In semi-natural habitats, vegetation structure, habitat features, such as microhabitat factors or management (grazing, mowing) and even ecological processes (e.g. the relationship between butterflies and ants) are important elements in determining the distribution of butterflies (Ravenscroft, 1994; Witek et al., 2006).

Maculinea butterflies are among the most intensively studied butterfly conservation model systems due to their special life cycle, endangered condition and because it is widely recognised that they are sensitive indicators of environmental change (New et al., 1995; Settele et al., 2005). Our study species, the Scarce Large Blue (*Macu-*

linea teleius, Bergsträsser, 1779), is an endangered butterfly throughout Europe (Van Swaay & Warren, 2003). Threats such as abandonment of traditional agriculture and habitat loss endanger the species in Hungary, although there are still several large populations (Bálint, 1991; Van Swaay & Warren, 2003). *M. teleius* breeds in wet meadows and oviposits in the flowerheads of its foodplant, Great Burnet (*Sanguisorba officinalis*). Therefore the butterfly's distribution strongly depends on the distribution of the host plant (Thomas, 1984). The species is obligately myrmecophilous (Thomas et al., 1989), the host ant species in the study area is *Myrmica scabrinodis* (Ylander, 1846) (Tartally & Csősz, 2004; Csősz et al., unpubl.). Young caterpillars – after developing to the final larval stage in the flowerheads of Great Burnet – are adopted by their host ants (Thomas, 1984). In the ant nests the caterpillars live as social parasites, i.e. prey on the ant brood until they complete their development the following year.

Figurny & Woyciechowski (1998) observed that *M. teleius*, in contrast to the sympatric species *M. nausithous* (Bergsträsser, 1779), oviposits on the younger and shorter flowerheads that are closer to the ground and have fewer flowers. However, the abundance of flowerheads at an appropriate stage of developement can be greatly affected by management (Johst et al., 2006). The habitat requirements of the early stages (eggs or larvae) are usually nar-

---

* Both authos contributed equally to the paper.

731

rower and more specialised than that of the imago, so these stages determine the distribution of the butterfly (Ellis, 2003). Therefore, it is only when the niches of foodplant and host ant overlap that *Maculinea* populations persist, i.e. sufficient eggs must be laid within the foraging range of its host *Myrmica* colonies (Thomas et al., 1998).

We selected extensively grazed pastures around eight closely adjoining fens on the Hungarian Great Plain. The surrounding of each fen is characterised by a mosaic of swamp meadows, calcareous purple moorgrass meadows and salt steppes, which host different subpopulations of *M. teleius* (Kőrösi et al., unpubl.). Our aims were to describe the microhabitats available for the butterfly around the fens, to determine the factors that influence the presence and density of *M. teleius* and finally to investigate the relationship between host ant species and *M. teleius*.

MATERIAL AND METHODS

The study area is situated at Kunpeszér, on the Hungarian Great Plain (Central Hungary, Kiskunság National Park). In the study area the mean annual temperature is about 10.3°C and mean annual precipitation about 520 mm. This large area (some hundreds of hectares) is a mosaic of fens and meadows. The patchiness of the area is due to the variation in local topography affecting soil humidity. Fens, situated in the most humid and deepest depressions, are characterised by willow bushes and reed and are not suitable habitats for this butterfly. Eight fens of a comparable size were selected (mean = 2.8 ha, range = 0.8–5.4 ha). Around them four types of microhabitat were available for this butterfly: vegetation dominated by Narrowleaf Cattail (*Typha angustifolia*, hence Typha microhabitat), by Purple Loosestrife (*Lythrum salicaria*, Lythrum microhabitat), by Marsh Woundwort (*Stachys palustris*, Stachys microhabitat) and by Purple Moorgrass (*Molinia coerulea*, Molinia microhabitat). The study area had been grazed by cattle for at least 5 years from early spring until late autumn. The cattle density was about 0.3 cows per hectare, and the grasslands were never fertilised or treated with pesticides.

Five 50 m long and 5 m wide transects were laid out at each marshland fen, from the edge of the fen perpendicularly outwards to the meadows and as far as possible from each other (Fig. 1). Transects were divided into ten 5 × 5 m quadrats (400 quadrats in total). The number of *M. teleius* individuals was recorded in each quadrat by walking along each transect in 2 minutes, usually twice a day (when weather conditions allowed) during the flight period from 31st of July to 25th of August in 2005, i.e. altogether 28 times. Observations on butterflies were carried out on relatively sunny, calm days, the first from 9:00 a.m. in the morning and second in the afternoon up to 4:00 p.m. Parallel to this study the basic population parameters of *M. teleius* were surveyed at the most populated fen (fen "A", see Fig. 1) using the MRR method. The daily number of individuals was about 500–700 and the population at fen "A" was around 2000 individuals, which means that the whole study area could support several thousands butterflies (Örvössy et al., unpubl.).

During the flight period we measured or assessed some local factors in the quadrats, which might be in association with the presence and density of the study species. We counted the number of foodplant flowerheads, measured soil humidity and vegetation height, and classified microhabitat type and grazing intensity in every quadrat. Soil humidity was based on a measure of the electrical conductivity at the end of the flight
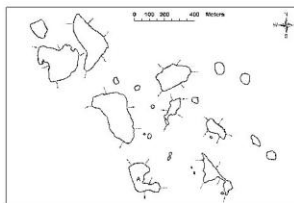

Fig. 1. Map of the study area. The fens are outlined by black lines, while the dashed lines indicate the transects. In the middle of the bottom part of the map is the most heavily populated fen (fen "A").

period. Vegetation height was measured at five random points in each quadrat and means of these measurements were used in the analyses. Grazing intensity was classified as absent, light or strong, based on the incidence of chewing and trampling. Furthermore, pitfall traps containing glycol were used to detect the presence of host ant species. One trap was placed in every second quadrat for two weeks shortly after the flight period. Thirty-two of the traps were lost due to trampling by cattle.

Since the species was not present in 209 quadrats, a logistic regression analysis was used to determine the relationship between presence of butterflies and explanatory variables. A nested design was used with transects nested within fens and quadrats within transects. A forward manual stepwise selection was made, and the null model had the presence-absence of the butterfly as the dependent variable, the number of foodplant flowerheads as the first covariate and fen and transect as random factors. Then, one by one all variables (soil humidity, grazing category, microhabitat type and vegetation height) were added until the best model was obtained (one with the smallest AIC value). Further, we took into account that the quadrats within a transect probably are not correlated equally with each other. Therefore, a correlation between the quadrats was built into the models, which were nested in transects. In this way it was possible to avoid edge effects causing bias in the models.

In the case of fen "A", where the most butterflies were observed, a linear regression analysis was carried out. The $\log_{10}$ transformation of the number of butterflies observed per quadrat was the dependent variable. The null model contained the number of foodplant flowerhead as the first covariate, the transect as a random factor and the above described correlation. Then the same forward manual stepwise selection procedure was applied as in the case of the logistic regression.

The comparisons between microhabitat types and distance from the fen, soil humidity, foodplant flowerhead density and vegetation height were tested using the Kruskal-Wallis test. The relationship between the number of *Maculinea teleius* and *Myrmica scabrinodis* was analysed using a Mann-Whitney test. All statistical analyses were performed using R software packages (R Development Core Team, 2004).

RESULTS

The position of the microhabitat types depends on the distance from the fen, usually in the order Typha microhabitat (edge of the fen), Lythrum microhabitat, Stachys
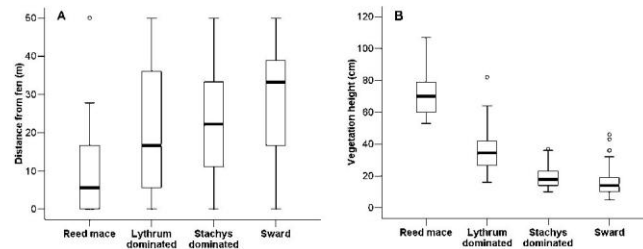
Fig. 2. Medians, quartiles and ranges of the four microhabitat types in terms of distance from a fen (A) and vegetation height (B). The circles indicate outliers.

microhabitat and Molinia microhabitat, furthest from the fen (Fig. 2a). This distribution is not a rigid one, as some of the microhabitats may not be present or not in this order. There are significant differences in the distances of four microhabitats from the edge of the fens (Kruskal-Wallis test; $\chi^2 = 55.2$, d.f. = 3, p < 0.001). This is due to differences in topography and soil humidity. There are significant differences in soil humidity (Kruskal-Wallis test; $\chi^2 = 176.6$, d.f. = 3, p < 0.001) and vegetation height among microhabitats ($\chi^2 = 235.4$, d.f. = 3, p < 0.001). The highest vegetation was at the edges of fens and declined along the transects as microhabitat types changed (Fig. 2b). The foodplant flowerhead density was significantly higher in the Lythrum and Stachys than in Typha and Molinia microhabitats ($\chi^2 = 62.1$, d.f. = 3, p < 0.001).

The best nested logistic regression model showed a significant effect for microhabitat type, but no effect of foodplant or grazing (Table 1). *M. teleius* seemed to prefer Stachys and Molinia microhabitats, where the butterfly was recorded in more of the quadrats, than in the Lythrum and Typha microhabitats, which were much less preferred (Fig. 3).

Altogether, there were obtained 553 individual sightings of butterflies, 290 were at the most populated fen (fen "A"). In the best linear regression model butterfly abundance was affected significantly by the number of foodplant flowerheads but not by grazing (Table 1). The abundance of *M. teleius* increased with the number of flowerheads (Table 1, Fig. 4).

Over the whole area the number of *M. teleius* was significantly higher in quadrats where host ants (*Myrmica scabrinodis*) were present compared to quadrats lacking the host ant (Mann-Whitney test, U = 2612.5, p = 0.003).

DISCUSSION

In this study microhabitat type was the most important factor determining the presence of *M. teleius* imagos in a large mosaic landscape (Stachys microhabitats were the most preferred), whereas at the most populated fen, only the density of foodplant flowerheads influenced the abundance of butterflies. However, the foodplant density was different in the microhabitats, the highest density occurred in Stachys and Lythrum microhabitats. This also means that the drier and shorter Molinia microhabitats, which were generally furthest from the fens and the wetter and higher Typha microhabitats close to the fens probably simply act as a matrix for the butterflies. Thomas & Elmes (2001) found that the foodplants preferred by *M. teleius* were most abundant in short (0–30 cm) vegetation in France and Poland. This is similar to our results, as in the Stachys microhabitat the range in vegetation height was 10–36 cm for the whole area, while at the fen "A" it was 16–34 cm and in the Lythrum microhabitat 22–44 cm. So this butterfly species seems to have similar vegetation height requirements in this region as in

TABLE 1. Effects of foodplant flowerhead density, grazing, microhabitat type, soil humidity and vegetation height on the presence (logistic regression) and abundance (linear regression) of *M. teleius* based on the transect counting method. The best models, after forward manual stepwise model selection do not contain all the explanatory variables. The results for the logistic regression were derived from all 40 transects at the eight fens, while the linear regression used only the data for the fen where the butterflies were most frequently recorded. Variance components of the logistic and linear regression models: random effect = 0.780, residuals = 0.934; random effect = 0.262, residuals = 0.271.

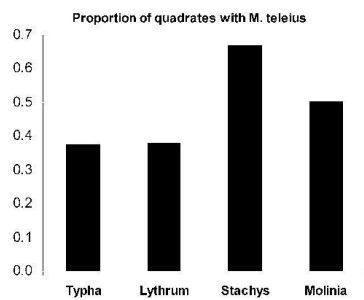|	Logistic regression				Linear regression			
	numDF	denDF	F	p	numDF	denDF	F	p
Foodplant flowerhead	1	354	0.008	0.928	1	42	10.956	0.002
Grazing	2	354	1.229	0.294	1	42	1.018	0.370
Microhabitat type	3	354	2.846	0.038				

Fig. 3. Proportion of quadrats on each of the four microhabitats in the whole study area where *M. teleius* was present.

Fig. 4. Relationship between number of foodplant flowerheads per quadrate and the logarithm of *M. teleius* abundance at the most heavily populated fen. The solid line represents the fixed effect of the linear mixed model.

other parts of Europe. Furthermore, with increase in foodplant density the abundance of butterflies increased at the most populated fen. In contrast to our result, which comes from one fen, Nowicki et al. (2005a) found that at a metapopulation level foodplant density limits the abundance of *M. alcon* [(Denis & Schiffermüller), 1775], but not that of *M. teleius* and *M. nausithous*, while Loritz & Settele (2005) showed that foodplant availability affects *M. nausithous* occupancy. Furthermore, Anton et al. (2005) showed that the density of *M. nausithous* is positively correlated with the density of its host ant *M. rubra* (L., 1758), but not with that of its foodplant *S. officinalis*. Our result can be explained by butterflies occurring mainly at those sites where their foodplants are abundant. However, microenvironmental factors (e.g. soil humidity) determine foodplant abundance and type of microhabitat, so microenvironmental factors and microhabitat types probably have direct and indirect effects on the butterfly.

For the conservation of endangered species, it is important to maintain the quality of this remaining habitats (Maes et al., 2004; WallisDeVries, 2004, Johst et al., 2006). The present study did not indicate that local grazing intensity had a direct effect on butterfly occurrence or abundance. We did not compare sites with different grazing intensity or regimes as in other studies (e.g. Griebeler & Seitz, 2002; WallisDeVries, 2004), because the whole area was subject to the same management, but measured grazing by means of indicators of chewing and trampling by cattle. However, the low grazing pressure recorded is probably adequate management for this study site. Therefore, like others (Thomas, 1990; Griebeler & Seitz, 2002), we also think that grazing results in a particular vegetation height and cover of grassland favourable for the butterfly and especially its host ants.

Van Dyck et al. (2000) concluded that host-ant nests (either directly or indirectly) could influence oviposition in *M. alcon*. Thomas & Elmes (2001) did not accept that *M. alcon* can detect ant nests before oviposition. The fact that th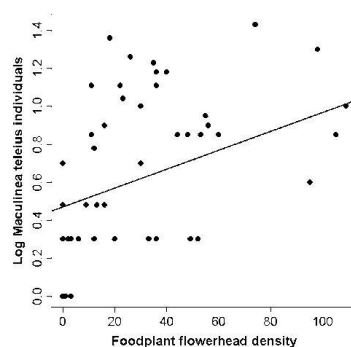ere was not an ant trap in each quadrat prevented the inclusion of host ant presence in the models and so it was only possible to test separately the relationship between host ant presence and *M. teleius* abundance. Though butterfly abundance was significantly higher in quadrats in which the host ant was present, this study is too limited to decide if this butterfly is directly or indirectly affected by the presence of host ants. But we draw attention to the fact that lower host ant density can increase the risk of local extinction (Thomas, 1994). However, most studies do not find a significant relationship between host ant presence and abundance of *Maculinea* imagos or eggs (e.g. Bonelli et al., 2005; Musche et al., 2005; Nowicki et al., 2005b; Prondvai et al., 2005; but see Anton et al., 2005; Glinka & Settele, 2005).

The implication for conservation is that grazing should be continued in order to maintain the current distribution of microhabitats. However, it must be emphasised that the grazing intensity in this study was about 0.3 cattle/ha, which is lower than the scheme prescribed in the current Hungarian Agri-Environment Program (0.5–1.2 cattle/ha depending on pasture productivity, Ángyán et al., 2003).

REFERENCES

ÁNGYÁN J., TARDY J. & VAJNÁNÉ-MADARASSY A. (eds) 2003: *Essentials of Farming on Protected and Environmentally Sensitive Areas*. Mezőgazda, Budapest, 625 pp. [in Hungarian])

ANTON C., MUSCHE M., HULA V. & SETTELE J. 2005: Which factors determine the population density of the predatory butterfly Maculinea nausithous? In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 57–59.

BÁLINT Z. 1991: Conservation of Butterflies in Hungary. *Oedippus*. **3**: 5–36.

BONELLI S., CROCETTA A., BARBERO F. & BALLETTO E. 2005: Oviposition behaviour in the myrmecophilous butterfly Maculinea alcon (Lepidoptera: Lycenidae). In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 65–68.

ELLIS S. 2003: Habitat quality and management for the northern brown argus butterfly Aricia artaxerxes (Lepidoptera: Lycaenidae) in North East England. *Biol. Conserv.* **113**: 285–294.

FIGURNY E. & WOYCIECHOWSKI M. 1998: Flowerhead selection for oviposition by females of the sympatric butterfly species Maculinea teleius and M. nausithous (Lepidoptera: Lycenidae). *Entomol. Gener.* **23**: 215–222.

GLINKA U. & SETTELE J. 2005: The effect of ant communities and spatial pattern for Maculinea nausithous. In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, p. 72.

GRIEBELER E.M. & SEITZ A. 2002: An individual based model for the conservation of the endangered Large Blue Butterfly, Maculinea arion (Lepidoptera: Lycaenidae). *Ecol. Model.* **156**: 43–60.

JOHST K., DRECHSLER M., THOMAS J. & SETTELE J. 2006: Influencing of mowing on the persistence of two large blue butterfly species. *J. Appl. Ecol.* **43**: 333–342.

KÉRY M., MATTHIES D. & FISCHER M. 2001: The effect of plant population size on the interactions between the rare plant Gentiana cruciata and its specialized herbivore Maculinea rebeli. *J. Ecol.* **89**: 418–427.

KONVIČKA M., HULA V. & FRIC Z. 2003: Habitat of pre-hibernating larvae of the endangered butterfly Euphydryas aurinia (Lepidoptera: Nymphalidae): What can be learned from vegetation composition and architecture? *Eur. J. Entomol.* **100**: 313–322.

KÜHN E., FELDMANN R., THOMAS J. & SETTELE J. 2005: *Ecology and Conservation of Butterflies in Europe. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 1.* Pensoft, Sofia, 128 pp.

LORITZ H. & SETTELE J. 2005: Effects of human land-use on availability and quality of habitats of the Dusky Large Blue butterfly. In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 225–227.

MAES D., VANREUSEL W., TALLOEN W. & VAN DYCK H. 2004: Functional conservation units for the endangered Alcon Blue butterfly Maculinea alcon in Belgium (Lepidoptera: Lycaenidae). *Biol. Conserv.* **120**: 229–241.

MUSCHE M., ANTON C., WORGAN A. & SETTELE J. 2005: Do ant cues influence the oviposition preference in the myrmecophilous Maculinea nausithous? In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 80–81.

NOWICKI P., PĘPKOWSKA A., KUDŁEK J., SKÓRKA P., WITEK M. & WOYCIECHOWSKI M. 2005a: Landscape scale research in butterfly population ecology – Maculinea case study. In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 140–143.

NOWICKI P., WITEK M., SKÓRKA P., SETTELE J. & WOYCIECHOWSKI M. 2005b: Population ecology of the endangered butterflies Maculinea teleius and M. nausithous and the implications for conservation. *Popul. Ecol.* **47**: 193–202.

NEW T.R., PYLE R.M., THOMAS J.A., THOMAS C.D. & HAMMOND P.C. 1995: Butterfly conservation management. *Annu. Rev. Entomol.* **40**: 57–38.

PRONDVAI E., KASSAI F., CSÖSZ S., ÁRNYAS E., BERECZKI J., TÓTH A., VARGA Z., PEREGOVITS L. & KIS J. 2005: Oviposition in Maculinea alcon butterflies. In Settele J., Kühn E. & Thomas J.A. (eds): *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, pp. 82–83.

R DEVELOPMENT CORE TEAM 2004: R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna; URL: http://www.R-project.org.

RAVENSCROFT N.O.M. 1994: The ecology of chequered skipper butterfly Carterocephalus palaemon in Scotland. I. Microhabitat. *J. Appl. Ecol.* **31**: 613–622.

SETTELE J., KÜHN E. & THOMAS J.A. 2005: *Species Ecology along a European Gradient: Maculinea Butterflies as a Model. Studies on the Ecology and Conservation of Butterflies in Europe. Vol. 2.* Pensoft, Sofia, 289 pp.

TARTALLY A. & CSÖSZ S. 2004: Data on the ant hosts of the Maculinea butterflies (Lepidoptera: Lycenidae) of Hungary. *Termvéd. Közl.* **11**: 309–317 [in Hungarian, English abstract].

THOMAS J.A. 1984: The behaviour and habitat requirement of Maculinea nausithous (the Dusky Large Blue Butterfly) and M. teleius (the Scarce Large Blue) in France *Biol. Conserv.* **28**: 325–347.

THOMAS J.A. 1990: Rare species conservation: case studies of European butterflies. In Spellerberg I.F., Goldsmith F.B. & Morris M.G. (eds): *The Scientific Management of Temperate Communities for Conservation*. Blackwell Scientific Publications, Oxford, pp. 149–197.

THOMAS J.A. 1994: The ecology and conservation of Maculinea arion and other European species of large blue. In Pullin A. (ed.): *Ecology and Conservation of Butterflies*. Chapman & Hall, London, pp. 180–196.

THOMAS J.A. & ELMES G.W. 2001: Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus Maculinea. *Proc. R. Soc. Lond. (B)* **268**: 471–477.

THOMAS J.A., ELMES G.W., WARDLAW J.C. & WOYCIECHOWSKI M. 1989: Host specificity among Maculinea butterflies in Myrmica ant nests. *Oecologia* **79**: 452–457.

THOMAS J.A., CLARKE R.T., ELMES G.W. & HOCHBERG M.E. 1998: Population dynamics in the genus Maculinea (Lepidoptera: Lycenidae). In Dempster J.P. & McLean I.F.G. (eds): *Insect Populations*. Chapman & Hall, London, pp. 261–290.

Van Dyck H., Oostermeier J.G.B., Talloen W., Feenstra V., Van der Hidde A. & Wynhoff I. 2000: Does the presence of ant nests matter for oviposition to a specialized myrmecophilous Maculinea butterfly? *Proc. R. Soc. Lond. (B)* **267**: 861–866.

Van Swaay C.A.M. & Warren M.S. 1999: *Red Data Book of European Butterflies (Rhopalocera). Nature and Environment Series No. 99.* Council of Europe, Strasbourg, 260 pp.

Van Swaay C.A.M. & Warren M.S. 2003: *Prime Butterfly Areas in Europe: Priority Sites for Conservation.* National Reference Centre for Agriculture, Nature and Fisheries, Ministry of Agriculture, Nature Management and Fisheries, Wageningen, The Netherlands.

WallisDeVries M.F. 2004: A quantitative conservation approach for the endangered butterfly Maculinea alcon. *Conserv. Biol.* **18**: 489–499.

Witek M., Sliwinska E.B., Skórka P., Nowicki P., Settele J. & Woyciechowski M. 2006: Polymorphic growth in larvae of Maculinea butterflies, as an example of biennialism in myrmecophilous insects. *Oecologia* **148**: 729–733.

Zimmermann K., Fric Z., Filipová L. & Konvička M. 2005: Adult demography, dispersal and behaviour of Brenthis ino (Lepidoptera: Nymphalidae): how to be a successful wetland butterfly. *Eur. J. Entomol.* **102**: 699–706.

Structure and size of a threatened population of the False Ringlet *Coenonympha oedippus* (Fabricius, 1787) (Lepidoptera: Nymphalidae) in Hungary

Noémi Örvössy[1]*, Ágnes Vozár[2], Ádám Kőrösi[1], Péter Batáry[1,3] & László Peregovits[4]

[1] Animal Ecology Research Group of the Hungarian Academy of Sciences and the Hungarian Natural History Museum, Ludovika tér 2, H-1083 Budapest, Hungary
[2] Ministry of Environment and Water, State Secretariat for Nature and Environment Protection, Fő u. 44-50, H-1011 Budapest, Hungary
[3] Agroecology, Georg-August University, Waldweg 26, D-37073 Göttingen, Germany
[4] Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary

*Corresponding author: orvossy@zoo.zoo.nhmus.hu

Abstract

Butterflies react sensitively to changes in habitat quality. Their diversity has been decreasing in Europe due to habitat degradation, fragmentation, management changes and climate change. The False Ringlet (*Coenonympha oedippus*) is one of the 59 butterfly species protected in Hungary. The species occupies marshy meadows dominated by *Molinietum* vegetation. Besides drainage, inappropriate management can also deteriorate these habitats. Nowadays the butterfly remains present in a habitat complex in Hungary, at the north-western part of the Hungarian Great Plain and a newly (2009) rediscovered population in north-western Hungary. Mark–release–recapture method was used to estimate the population size and describe population structure in a 0.65 ha habitat patch from 2005 to 2007. The population size did not fluctuate during the 3 years; the total estimated number of individuals ranged between 130 and 270. The survival probability was 0.81–0.84/day in the case of males, in females 0.70–0.89/day. The catchability was between 0.27–0.53 in males and 0.22–0.38 in females. The structure of the population indicates that the False Ringlet is a sedentary butterfly species, with low dispersal ability. In the study area, drainage seems to be the main threatening factor for its habitat. The studied population has recently moved to neighbouring lower parts of the habitat patch, because the formerly occupied part of the habitat patch had been desiccated and the vegetation had been changed. For the long-term survival of the species at this habitat patch the drainage should be inhibited, while in other habitat patches around, the control of invasive plant species is inevitable beside habitat restoration.

Keywords: False Ringlet, *Coenonympha oedippus*, Hungary, MRR, population size

Introduction

The diversity of butterfly species has decreased in large volume in Europe, some surveys show even larger decrease, than in the groups of bird or plant species (e.g. Thomas et al. 2004). Similarly, the threat status of the species decayed more strongly among butterflies (Van Strien et al. 2009). The main reasons of butterfly diversity decline in Europe are habitat fragmentation (Ehrlich 1988, Maes & Van Dyck 2001), habitat loss (Pullin 2002) and changes of land management (Skórka et al 2007). Due to their sensitivity to temperature, climate change has also enhanced effect on the diversity of butterflies (Lewis & Bryant 2002, Settele et al. 2008).

Agricultural landscapes are affected by either intensification (Thomas 1995) or abandonement, both of which can diminish formerly suitable butterfly habitats (Strijker 2005). The succession after abandonment and the colonization of invasive alien species can decrease the diversity and abundance of native species (Skórka et al. 2007). Species inhabiting wet meadows are among the most endangered ones, because the area of those habitats is declining rapidly as they can be easily converted to agricultural landscapes (Maes & van Dyck 2001, Maes et al. 2004). Drainage is widely recognized as the most important threatening factor for wet meadows, which can affect large areas throughout water table equalization (IUCN 1993).

The False Ringlet (*Coenonympha oedippus*) inhabits wet meadows dominated by *Molinia* species. It is one of the most endangered butterflies in Europe; it is considered as nearly threatened by IUCN (2008) and listed in Annex II and IV of Habitats Directive and Annex II of the Bern Convention. The geographical distribution of the species is highly fragmented and colonies are isolated (Van Helsdingen et al. 1996, Kudrna 2002). The size and distribution of the European populations are declining at several localities and seem to be stable at others, while limited information is available about the populations in Asia.

One of the first publications about the species describes its weak, jumping flight, which is related to the supposed weak dispersal ability (Seitz 1906). The first description of the ecological requirements of the species is from France. Lhonore & Lagarde (1999) mention the problems of fragmentation, isolation and other threatening factors, which endanger the long-time survival of the butterfly. The size and structure of a Slovenian population was studied with mark–release–recapture method by Čelik (2004) from 1995 to 1996. The maximum density of the butterflies was 145 individuals/ha in a 1.27 ha habitat patch, which in contrast to other European habitats consists of areas of *Brachypodium* grasslands and shrubs. Survival probability was 0.77/day for males and 0.80/day for females in the second year (Čelik 2004).

In Hungary, there were several suitable habitat areas for the species earlier, e.g. remarkable populations were described from the Hanság, Kiskunság, Óbuda regions and from Szár according to specimens in the collection of the Hungarian Natural History Museum (Bálint et al. 2006). Due to large-scale drainage in the Kiskunság and Hanság, several wet meadows disappeared, hence their vegetations have been changed (Molnár et al. 2008). The Óbuda area (today the northern part of Budapest) was lost due to urban development.

There is a habitat complex left in the Kiskunság region, in the north-western part of the Hungarian Great Plain, near to Ócsa. However, extinction directly threatens the species in this habitat complex as well due to habitat deterioration and isolation. Habitat degradation is the result of drainage accompanied with aggressive dispersion of invasive plant species. The transformation of vegetation associations caused by desiccation can lead to the spread of invasive alien plant species (e.g. *Solidago* spp.), which are present around the area. In Eastern European wet meadows, *Solidago* spreads forcefully and affects negatively the butterfly communities (Moroń et al. 2009). Since the 1980's the butterfly has left some parts of the habitat, which have become unsuitable and it has moved to lower habitat patches. There was a large population at the Csiffári meadows 2.8 km from the study site (Seregélyes et al. 1986), but that area has become very dry recently and now it is covered by mesophilous vegetation instead of *Molinietum*.

The nearly threatened status of the species motivates the monitoring of the population size. However, to facilitate long-term survival of the species, more accurate population size estimation and the exploration of population structure are necessary. The aim of this study was to estimate some essential parameters of population dynamics (e.g. popula-

tion size, sex ratio, survival rate, average lifespan) in a single population of the False Ringlet in a three-year period using mark–release–recapture method.

Material and methods

Distribution

The distribution of the species is just partly documented; populations were probably widely distributed in the steppe zone of the temperate region, in *Molinietum* habitats. Outside Europe the species is present in temperate Asia as well: Ural, S and W Siberia, N Kazakhstan, Mongolia, China and Japan (Tolman & Lewington 2008). Based on the database of the IUCN the nearly threatened species is native in Austria, Belgium, France, Germany, Hungary, Italy, Japan, Kazakhstan, Liechtenstein, Mongolia, Poland, Russian Federation, Slovakia, Spain, Switzerland and Ukraine (IUCN 2008). The map of the "Encyclopedia of life" shows 18 localities in France, 8 in Italy, 8 in Austria, 5 in Liechtenstein, 4 in Poland, 2 in Switzerland, 2 in Spain and 1 in Hungary, based mainly on
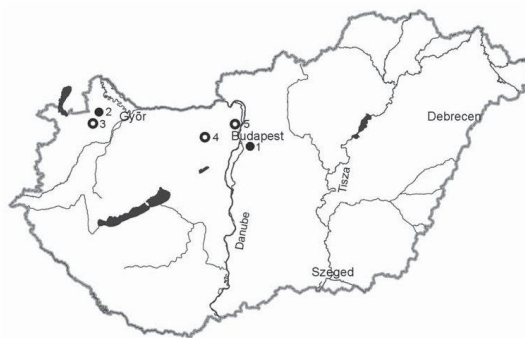
Fig. 1. Present (●) and former (○) populations of the False Ringlet in Hungary. 1 study site at Ócsa (Kiskunság region), 2 new population found in 2009 (Hanság), 3 Hanság, 4 Szár, 5 Óbuda.

data from museum collections. In Asia 2 localities in Japan and 1 in South Korea are known (EOL 2009). None of the databases contains information about the existing Croatian and Slovenian populations (Sasic, this volume, Čelik et al. this volume), for other countries the information is extremely incomplete, e.g. Italy had more than 100 populations (Bonelli et al. this volume).

In Hungary, former populations of the species existed in the Hanság, Óbuda and Kiskunság region (Fig. 1). The only present population was considered to be in the Kiskunság region, but in 2009 a new, unknown location was found in the north-western part of Hungary.

Study site

Our study site was 0.65 ha in size, covered with *Molinietum* vegetation and surrounded with bushes and trees (*Salix* spp.) The area tends to be overgrown by common reed (*Phragmites australis*), reed mace (*Typha* spp.) and willow (*Salix* spp.) shrubs. The traditional management was extensive mowing or light grazing. Presently the meadow is mown once in a couple of years. The water table level is lower than ideal due to two reasons. The drainage started in the 1920's (Seregélyes et al. 1986), while later on the advance of gravel mining accelerated the desiccation of the area. The butterfly population has recently moved to lower areas compared to the habitat maps from the 1980's (L. Peregovits personal observation).

Species

The species is strictly protected by law in Hungary, considered as nearly threatened by IUCN (2008). Part of its Hungarian habitats are strictly protected in the Ócsa Landscape Protected Area and designated as Sites of Community Interests. The False Ringlet has one generation in Hungary; the flight period is in June–July. Females lay eggs from late June. The polyphagous larvae hatch after 2–3 weeks and start feeding on *Molinia* and *Carex* species.

Sampling method

For population size estimation mark–release–recapture method was used in one habitat patch. Samplings occurred between 16th. June – 1st. July 2005, 17th. June – 7th. July 2006 and 6th. June – 20th. June 2007. The sampling effort

Table 1. Results of MRR: capture statistics for *Coenonympha oedippus* in 2005–2007 at Ócsa.

Year	No. of marked individuals		No. of recaptures		No. of captures	
	male	female	male	female	male	female
2005	70	66	139	95	209	161
2006	106	140	234	326	340	466
2007	58	42	26	12	84	54

1999). The total size of butterflies in a year was calculated with the modified method of Cook et al. (1967). The dominant grasses and sedges were identified in 2005 in the presently and formerly occupied habitat patches of the species.

Results

The number of marked, captured and recaptured males was higher than those of females in two years, females outnumbered males in capture statistics in 2006 (Table 1).

The model selection resulted gender dependent survival and capture probability in the first two years and gender independent survival and capture probability in the third year. Female survival probability was slightly higher than that of the males in 2005 and 2006. The survival probability in the third year was gender independent and decreased to 0.78. The mean lifespan of females was 8.58 and 7.18 days in the first years, while mean lifespan of males was 5.74 in 2005 and 5.04 in 2006. The mean lifespan had decreased to 3.95 for both sexes in 2007 (Table 2). Capture probability was 0.40 and 0.53 in males and 0.22 and 0.38 in the case of females in the first years and 0.27 in 2007 (Table 2). The estimated total population size was 137 in 2005, 273 in 2006 and 212 in 2007, for the intensive study years 2005 and 2006 this is close to the number of actually marked individuals (Tables 1 and 2).

**Table 2.** Results of MRR: population structure and parameter estimations.

Year	Daily survival probability ±SE		Mean lifespan		Capture probability ±SE		Estimated total population size	
	male	female	male	female	male	female	male	female
2005	0.84±0.02	0.89±0.02	5.74	8.58	0.4±0.04	0.22±0.03	67.85	69.71
2006	0.82±0.02	0.87±0.01	5.04	7.18	0.53±0.03	0.38±0.02	116.30	157.46
2007	0.78± 0.04		3.95		0.27±0.06		212.80	

was different in the three years: sampling was conducted daily in 2005 and 2006, while every second day in 2007. The butterflies were marked individually with permanent ink pen. A grid of 5×5 m quadrates was laid down in the habitat and capture locations were recorded.

The apparent survival probability and capture probability were estimated for both sexes with the Cormack–Jolly–Seber method using Mark 5.1 (White & Burnham 1999). The best models were selected based on Akaike's information criterion (AIC). Mean lifespan was calculated from survival probability (Cook et al. 1967). The daily population size was estimated with program POPAN 5 (Arnason & Schwarz

The highest estimated daily population size changed between 45–81 for males and 29–96 for females (Fig. 2). Males reached their maximum estimated daily population size earlier than females in each year. The butterfly showed the characteristics of protandry, males outnumbered females in the first days of the observation period (Figs. 2 and 3).

Observations of individual movements during the sampling suggested that the butterflies preferred the wettest areas, while avoided open spaces probably due to the more balanced microclimate in the vicinity of bushes; the individuals were sedentary, their flight was short and jumping. They performed short movements. The average distance between
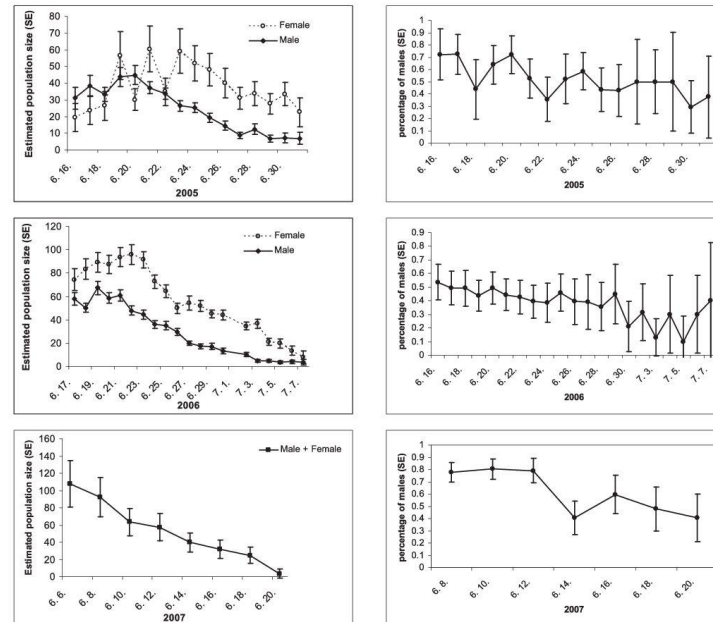
Fig. 2. Estimated daily population size in a habitat patch of *Coenonympha oedippus* from 2005 to 2007, based on MRR studies.

Fig. 3. Percentage of males based on daily capture exceeds female ratio during the first days of sampling in all the examined years.

Table 3. Plant species list in the recent and in the earlier habitat patch, the species composition is changing due to drainage.

	Recent habitat	**Earlier habitat**
Vegetation	species rich *Molinietum*	searing *Molinietum*, with mesophyl patches
Dominant grass species	*Deschampsia caespitosa, Molinia* sp., *Phragmites australis*	*Molinia* sp., *Festuca pratensis, Calamagrostis epigeios*
Dominant sedge species	*Carex acutiformis, Cladium mariscus, Schoenus nigricans*	
Characteristic attendant species	*Equisetum arvense, Inula britannica, Lythrum salicaria, Carex flacca, Cirsium palustre*	*Rhinanthus* sp., *Galium verum, Deschampsia caespitosa, Dactylis glomerata, Briza media*

consecutive recaptures was 38.3 m (52 animals, 1–11 movements/animal). According to the tracking data of individuals, males moved more frequently and flew longer distances (approx. 10–15 m/occasion) than females (0.2–4m), although sample size was not sufficient for statistical analysis.

In the presently occupied habitat patch a species rich *Molinietum* complex exists, while the neighbouring, formerly occupied part of the habitat shows characteristics of a mesophilous meadow with plenty of herbaceous plant species (Table 3).

Discussion

During the three years of the survey, there was no major fluctuation in population size, a promising sign regarding its survival, even though long–term trend cannot be estimated in this time scale. Along with Čelik's survey in Slovenia, protrandric population structure was observed (Čelik 2004), which is a widely recognized phenomenon among butterflies. Early eclosion of males minimizes the energy consumption of females and predation threats before reproduction, while males have enough time to seek for females (Ehrlich 1989). Both males' and females' movement was restricted to short-distance within the habitat patch, similar to Čelik's results (2004). Short flights imply sedentary living habits and closed population.

The apparent survival rate (0.78–0.89) of the species is in the higher region among butterflies. According to Brakefield (1982), survival probability around 0.8 is typical to butterfly species with colonial population structure in temperate climate zones. Although survival rate can be as high as 0.94 in other butterflies species, like *Euphydryas aurinia* (Schtickzelle et al. 2005); or 0.88 for males and 0.84 for females as in the case of *Lopinga achine* (Bergman & Landin 2002). Both butterflies' dispersal ability is similar to sedentary and vulnerable species (Bergman & Landin 2002, Schtickzelle et al. 2005). Our observations on within site movement do not contradict with these results, as the movement lengths of *Coenonympha oedippus* between two consecutive captures are generally short. We can confirm that survival rate around 0.8 might be a sign that the population is closed and dispersal of individuals is low. During 2005 and 2006, the survival rate of the females was higher than that of the males, which is in agreement with the results of Čelik (2004).

Decline of the survival rate in 2007 is a reason to worry, as the shorter lifespan of females can have a direct effect on the quantity of eggs laid. It's proven in the case of *M. rebeli* that the total quantity of eggs possibly laid can be many times higher than the realized number of eggs laid, in other words the females are time-constrained regarding their egg-laying (Kőrösi et al. 2008). Therefore, along with the decrease of the lifetime, the number of laid eggs probably decreases, making the basis of the next generation and the long-term survival of the population uncertain. However, the decline of the apparent survival rate can be a sign of growing dispersion too, because of the declining quality of the habitat patch or any other general problem, i.e. the paramount hot weather in June and July in 2007. The mean lifespan of males was 5 to 6, females 7 to 9 days in the first

years, which is slightly higher than estimated in the Slovenian population (Čelik 2004). But in 2007 the mean lifespan was similar to the Slovenian results (Čelik 2004).

It has particular importance that at the beginning of our sampling in 2005 the population was found in a different location, in a deeper site, than during the last surveys in the 80's. In this respect this fact warns of the danger of continuous desiccation. Vegetation contains *Molinia* tussocks only in the current habitat, while the previous habitat patch is now rather a meadow rich in mesophilous species. This is characteristic recently to the whole area – the formerly base-habitat of Csiffári rét (2.8 km form our study site; Seregélyes et al. 1986) has now a strongly desiccating *Astragalo–Festucetum*, where the butterfly is now absent. Assuming that this meadow had been a firmly wet *Molinietum*, the average groundwater level dropped with 20–40 cm since the 80's (Seregélyes et al. 1986).

Although the habitat complex of Ócsa lies within the borders of Duna–Ipoly National Park, the area is not exempt from human impact: there are some gravel pits in the vicinity of the strictly protected area. Gravel mining creates large-surfaced deep lakes, which load themselves with groundwater. As a result of evaporation, these lakes take groundwater from the surrounding areas, which dries them up and change the vegetation (Tari et al. 2008). The region is also well-drained, which causes a lower water retention ability and desiccation as well (Hubayné Horváth 2005).

Another threatening factor of the *Coenonympha oedippus* habitats is the advance of weeds and invasive plant species. Primarily, *Solidago* species occupy a growing percentage of the habitat complex, which could be controlled by regular mowing during flowering time (Weber 2000, Moroń et al. 2009). However, the complete elimination of *Solidago* seems to be unlikely. Wet meadows between groves of trees are used by hunting organizations as well, providing corn and other grains (containing weeds) for the game. This activity creates weed-communities, altering and deteriorating further the vegetation required by the butterfly.

In the absence of management, succession in this area will result in bushy groves, which is not appropriate for the butterflies. According to our observations butterflies also avoid large open areas. To apply appropriate conservation management it is inevitable to learn more about the butterfly's habitat use, considering the different aspects of requirements of all life stages (Dennis et al. 2006, Vanreusel & Van Dyck 2007).

In Hungary *Coenonympha oedippus* is present in this habitat complex and a newly discovered population in north-western Hungary only. Part of the formerly known habitats are vanished, such as those around Óbuda and Szár, other parts are now being reconstructed, such as those in Hanság (Margóczi et al. 2002). There are some areas in the Kiskunság National Park that seem to be appropriate for the butterfly. The isolation of the remained populations (among them this surveyed one) with small size indicates the possibility of inbreeding, which should be excluded or confirmed by genetic surveys. Accordingly, we conclude that the development of conservation actions for *Coenonympha oedippus* is essential and inevitable. Habitat degradation should imme-

diately be stopped, especially the desiccation, and the spread of invasive plants should be controlled, to maintain proper habitats for long-term survival of the species in Hungary.

Acknowledgement

References

Arnason N, Schwarz CJ (1999) Using POPAN-5 to analyse banding data. *Bird Study* 46 (Suppl.): 157-168.

Bálint Z, Gubányi A, Pitter G (2006) *Magyarország védett pillangóalakú lepkéinek katalógusa a Magyar Természettudományi Múzeum gyűjteménye alapján* [A catalogue of protected papilioformid butterflies of Hungary based on the collection of the Hungarian Natural History Museum]. Hungarian Natural History Museum, Budapest.

Bergman KO, Landin J (2002) Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation* 108: 361–369.

Brakefield PM (1982) Ecological studies on the butterfly Maniola jurtina in Britain. II. Population dynamics: the present position. *Journal of Animal Ecology* 51: 721-738.

Čelik T (2004) Population dynamics of endangered species Coenonympha oedippus Fabricius, 1787 (Lepidoptera: Satyridae) on the Ljubljansko Baarje (Slovenia). *Acta Entomologica Slovenica* 12: 99-114.

Convention on the Conservation of European Wildlife and Natural Habitats CETS No.: 104.

Cook LM, Brower LP, Croze HJ (1967) The accuracy of a population estimation from multiple recapture data. *Journal of Animal Ecology* 6: 57-60.

Dennis RLH, Shreeve T, Van Dyck H (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity Conservation* 15: 1943-1966.

Ehrlich PR (1988) The loss of diversity: Causes and consequences. In: Wilson EO, Peter FM (eds) *Biodiversity*. National Academy Press, Washington D.C, pp. 212–216.

Ehrlich PR (1989) The structure and dynamics of butterfly populations. In Vane-Wright RI, Ackery PR (eds) *The Biology of Butterflies*. Princeton University Press, Princeton, 25-40.

EOL (2009) "Coenonympha oedippus Fabricius, 1787." Encyclopedia of Life, available from http://www.eol.org/pages/965969?vetted=true&category_id=9 Accessed 15 May 2009.

World Conservation Monitoring Centre (1996) Coenonympha oedippus. In: IUCN 2008.

Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora) Official Journal L 206, 22/07/1992 P. 0007 – 0050; (http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML)

Hubayné Horváth N (2005) Felhagyott tőzegkitermelő-helyek természeti értékei és optimális hasznosítása. [Natural values of a cutaway peatlands and their optimal after-use] PhD Dissertation, Budapesti Corvinus Egyetem, Tájtervezési és Területfejlesztési Tanszék, Budapest

IUCN (1993) The wetlands of Central and Eastern Europe. *The World Conservation Union. IUCN East European Programme, Environmental research Series* 7. pp. 83.

IUCN (2008) Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 15 May 2009.

Kőrösi Á, Örvössy N, Batáry P, Kövér Sz, Peregovits L (2008) Restricted within-habitat movement and time-constrained egg-laying of female *Maculinea rebeli* butterflies. *Oecologia* 156 (2): 455-464.

Kudrna O (2002) The Distribution Atlas of European Butterflies. *Oedippus* 20: 1-343.

Lewis OT, Bryant SR (2002) Butterflies on the move. *TRENDS in Ecology & Evolution* 17: (8) 351-352.

Lhonore J, Lagarde M (1999) Biogeography, ecology and conservation of Coenonympha oedippus (Fab., 1787) (Lepidoptera: Nymphalidae: Satyrinae) *Annales de la Societe Entomologique de France* 35: 299-307.

Maes D, Van Dyck H (2001) Butterfly diversity loss of Flanders (North Belgium): Europe's worst case scenario? *Biological Conservation* 99: 263-276.

Maes D, Vanreusel W, Talloen W, Van Dyck H (2004) Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). *Biological Conservation* 120: 229-241.

Margóczi K, Takács G, Pellinger A, Kárpáti L (2002): Wetland reconstruction in Hanság area (Hungary). *Restoration Newsletter* 15: 14-15.

Molnár Z, Bíró M, Bölöni J, Horváth F (2008) Distribution of the (semi)-natural habitats in Hungary I. – Marshes and grasslands. *Acta Botanica Hungarica* 50 (Suppl): 59-105.

Moroń D, Lenda M, Skórka P, Szentgyörgyi H, Settele J, Woyciechowski M (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation* 142: 1322-1332.

Pullin AS (2002) *Conservation biology*. Cambridge University Press, Cambridge, UK. 358pp.

Schtickzelle N, Choutt J, Goffart P, Fichefet V, Baguette M (2005) Metapopulation dynamics and conservation of the marsh fritillary butterfly: Population viability analysis and management options for a critically endangered species in Western Europe. *Biological Conservation* 126: 569–581.

Seitz A (1906) *The Macrolepidoptera of the Palearctic Region 1*. Stuttgart, 379pp.

Seregélyes T, Pallag O, Grofcsik Gy (1986) Az Ócsai Tájvédelmi Körzet természetvédelmi fenntartási és fejlesztési terve. [*Nature sustainance and development plan for the Ócsa Landscape Protection Area.*] Környezetvédelmi Intézet, Budapest, 49pp.

Settele J, Kudrna O, Harpke A, Kühn I, van Swaay I, Verovnik R, Warren M, Wiemers M, Hanspach J, Hickler T, Kühn E, van Halder I, Veling K, Vliegenthart A, Wynhoff I, Schweiger O (2008) *Climatic Risk Atlas of European Butterflies. BioRisk* 1: 1-710.

Skórka P, Settele J, Woyciechowski M (2007) Effects of management cessation on grassland butterflies in southern Poland. *Agriculture, Ecosystems & Environment* 121: 319-324.

Strijker D (2005) Marginal lands in Europe–causes of decline. *Basic and Applied Ecology* 6: 99-106.

Tari C, Szanyi J, Kovács B (2008) A Ráckevei – Duna és az Ócsai Tájvédelmi Körzet között elhelyezkedő kavicsbányák hidraulikai hatásai. [*Hidraulical effects of the gravel mines located between the Danube of Ráckeve and the Ócsa Landscape Protection Area*] *Abstract Meeting of Young Geoscientist* http://isza.hu/index.php?searchword=%F3csa&option =com_search&Itemid=5

Thomas JA (1995) The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society* 56 (Suppl.): 55–72.

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303: 1879–1881.

Tolman T, Lewington R (2008) *Collins Butterfly Guide*. Harper Collins Publishers, London, 384pp.

Van Helsdingen PJ, Willemse L, Speight MCD (1996) *Background information on invertebrates on the Habitats Directive and the Bern Convention*, Council of Europe, 217pp.

Vanreusel W, Van Dyck H (2007) When functional habitat does not match vegetation types: A resource–based approach to map butterfly habitat. *Biological Conservation* 135: 202–211.

Van Strien AJ, van Duuren J, Foppen RPB, Soldaat LL (2009) A typology of indicators of biodiversity change as a tool to make better indicators. *Ecological Indicators* 9(6): 1041-1048.

Weber E (2000) Biological flora of central Europe: *Solidago altissima. L. Flora* 195: 123-134.

White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.): 120-138.

ORIGINAL PAPER

Potential metapopulation structure and the effects of habitat quality on population size of the endangered False Ringlet butterfly

Noémi Örvössy · Ádám Kőrösi · Péter Batáry · Ágnes Vozár · László Peregovits

Abstract The False Ringlet (*Coenonympha oedippus*) is a European butterfly species, endangered due to the severe loss and fragmentation of its habitat. In Hungary, two remaining populations of the butterfly occur in lowland Purple Moorgrass meadows. We studied a metapopulation occupying twelve habitat patches in Central Hungary. Our aim was to reveal what measures of habitat quality affect population size and density of this metapopulation, estimate dispersal parameters and describe phenology of subpopulations. Local population sizes and dispersal parameters were estimated from an extensive mark–release–recapture dataset, while habitat quality was characterized by groundwater level, cover of grass tussocks, bush cover, height of vegetation and grass litter at each habitat patch. The estimated size of the metapopulation was more than 3,000 individuals. We estimated a low dispersal capacity, especially for females, indicating a very low probability of (re)colonization. Butterfly abundance and density in local populations increased with higher grass litter, lower groundwater level and larger area covered by tussocks. We suppose that these environmental factors affect butterfly abundance by determining the microclimatic conditions for both larvae and adult butterflies. Our results suggest that the long-term preservation of the studied metapopulation needs the maintenance of high quality habitat patches by appropriate mowing regime and water regulation. Management also should facilitate dispersal to strengthen metapopulation structure with creating stepping-stones or gradually increase habitat quality in present matrix.

Keywords *Coenonympha oedippus* · Dispersal · Habitat management · Mark-recapture · Population size · Purple Moorgrass meadow

Introduction

The biodiversity crisis currently seems to appear more critical among butterfly species than other species (Thomas 1991; Thomas et al. 2004). Butterfly populations disappear more rapidly than bird or plant populations due to short life and lack of dormant propagules (Thomas et al. 2004). However, Hambler et al. (2011) suggested that long-term extinction rates are similar amongst birds and butterflies, but the latter react more rapidly to changes in habitat quality or climate. In Europe, the decline is attributed to habitat destruction, agricultural intensification or abandonment and climate change (Thomas 1991; Thomas and Morris 1994; Warren et al. 2001; Hanski 2003; Parmesan 2003). As European landscapes have long been human dominated, many species rich habitat types rely on low-intensity agricultural use typical of earlier agronomic eras, now requiring conservation-oriented habitat management

N. Örvössy (✉) · L. Peregovits
Hungarian Natural History Museum, Baross utca 13, 1088 Budapest, Hungary
e-mail: orvossyn@gmail.com

Á. Kőrösi · P. Batáry
MTA-ELTE-MTM Ecology Research Group, Pázmány P. s. 1/C, 1177 Budapest, Hungary

P. Batáry
Agroecology, Georg-August University, Grisebachstr. 6, 37077 Göttingen, Germany

Á. Vozár
Natura 2000 Unit, Department of Nature Conservation, State Secretariat for Environmental Affairs, Ministry of Rural Development, Kossuth tér 11, 1055 Budapest, Hungary

🌀 Springer

to maintain them. Around 50 % of butterfly species live in such semi-natural managed grasslands (Erhardt and Thomas 1991), where management is necessary to maintain their current populations (van Swaay and Warren 1999; van Swaay 2002).

Wet meadows are seriously threatened by the above factors (Halada et al. 2011), and have become one of the most endangered habitat types in Europe. Habitat degradation and fragmentation of wet meadows have caused the decline of several butterflies (van Swaay and Warren 1999; Nowicki et al. 2007; Skórka et al. 2007), including the False Ringlet (*Coenonympha oedippus*) (van Swaay et al. 2010). Most of its European populations are threatened by habitat loss (isolation and fragmentation) and habitat degradation, especially land drainage, abandonment and changes in habitat management. Populations also suffer from the spread of invasive weeds (*Solidago* spp.) and encroachment of bushes after abandonment, collection of butterflies, development of built-up areas and climate change (van Swaay and Warren 1999; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010).

In order to stop further decline and promote the long-term survival of the species, suitable habitat management is required. Development of a proper management action plan should be based on a survey that describes which factors influence the metapopulation structure of the species under consideration and determine the parameters of the best available habitat's quality.

Generally, two main approaches exist to explain the variation of population size and predict survival of butterfly species: metapopulation theory and the habitat quality approach (Thomas et al. 2001). Metapopulation theory assumes that patch size and isolation are the main factors that influence population size and persistence in a habitat patch (Hanski and Glipin 1997), which has been supported by several studies (e.g. Thomas and Hanski 1997; Thomas et al. 1998; Nowicki et al. 2007). This approach has been used for several butterfly species due to their high sensitivity to fragmentation (Baguette and Nève 1994; Hanski 1998; Fischer et al. 1999; Öckinger 2006; Hovestadt et al. 2011). However, the metapopulation approach has some limitations in continuous landscapes, where habitat patch definition is not exact and resources of butterflies do not spatially overlap (Dover and Settele 2009).

The resource limitation approach offers an alternative to avoid the problems of patch definition, continuity of landscapes and sparse location of resources in the matrix (Dennis et al. 2006). It determines the habitat based on necessary resources, and emphasises the importance of the habitat quality (Vanreusel and Van Dyck 2007). The resource limitation approach is part of the wider and more traditional habitat quality approach, which is the analysis of habitat quality in light of the habitat requirements of a

certain species (Oostermeijer and van Swaay 1998; Skórka et al. 2007). Such studies usually include surveys to determine appropriate habitat management. Using both metapopulation and habitat quality approaches in the same study, it is possible to predict population size or density (Thomas et al. 2001; Sawchik et al. 2003; Rabasa et al. 2008) and in some cases patterns of site occupancy more reliably than by the conventional separation (Lenda and Skórka 2010; Sanford et al. 2011). Furthermore, this double approach is particularly relevant in the study area, as the False Ringlet lives in a fragmented habitat complex where habitat quality varies considerably. Efforts to maintain the small and isolated populations by conservation management are hampered by a lack of knowledge about the habitat requirements of this species. Hence, a suitable management regime would facilitate the long-term survival of the species. Therefore, our study aims were (i) to gain information about the population structure: discriminate clusters based on phenology, asynchrony of subpopulations and movement pattern of the species, and (ii) to determine whether and how habitat quality affect its population size and density.

Materials and methods

Species

The distribution area of the False Ringlet covers the whole Palaearctic region (Gorbunov 2001; Bozano 2002). The locations of European populations are more or less identified, while there is little information about the Asian populations. The current geographical distribution of the species is highly fragmented, and colonies in the European part are highly isolated (Kudrna 2002). The species has experienced more than 80 % population decline across its European range in recent decades, and has become extinct in Slovakia, Bulgaria and Switzerland (van Swaay and Warren 1999; Dušej et al. 2010). The False Ringlet is considered as "near threatened" by IUCN (2011), and is listed in Annex II and IV of the Habitats Directive and Annex II of the Bern Convention. Although the size and distribution of the European populations are declining at several localities, some populations seem to be stable. The largest and most stable populations exist in Italy (Bonelli et al. 2010). Highly isolated populations are still present in France (Lhonoré and Lagarde 1999), Liechtenstein (Staub and Aistleitner 2006), Austria (Aistleitner et al. 2006), Slovenia (Čelik and Verovnik 2010), Croatia (Kučinić et al. 1999; Šašić 2010), Hungary (Örvössy et al. 2010), Poland (Sielezniew et al. 2010) and Russia (Gorbunov 2001). Outside Europe, *C. oedippus* is very abundant in the Transbaikalia, northern Altai, Chuluunbaatar and in the Mongolian Altai, while populations are more scattered

in the West Siberian lowlands (Gorbunov and Kosterin 2007, Bräu et al. 2010). The European populations generally occupy semi-open wet habitats: Purple Moorgrass (*Molinia coerulea*) meadows, bogs, wet heathlands, sedge communities at marginal zones of swamps and forest meadows (Bräu et al. 2010; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010). There are some populations in the Mediterranean parts of Europe that occur in dry habitats (Čelik 2004; van Halder et al. 2008), but also with a high coverage of Purple Moorgrass. In Hungary, the species has been recorded in several locations, but its original habitats have disappeared or decreased in size. There are only two remaining metapopulations, the current study site at Ócsa, Central Hungary (Örvössy et al. 2010) and one in the Fertő-Hanság National Park, Western Hungary (András Ambrus pers. comm.)

Based on earlier studies of within-habitat movements, this species was considered sedentary with weak flight ability (Lhonoré and Lagarde 1999; Celik et al. 2009). Its oviposition is not selective, as females lay their eggs on different plant species or on grass litter (Bräu et al. 2010). After emergence, young polyphagous larvae feed on monocotyledonous species, especially on Purple Moorgrass (Bräu et al. 2010). Larvae hibernate in the tussocks of grass, continue feeding during spring and pupate in early May (Bräu et al. 2010). Imagoes emerge in June–July, and the flight period lasts 4–5 weeks.

Study site

Our study area was situated next to the town of Ócsa, Central Hungary, and belongs to the Duna-Ipoly National Park. All potential habitat patches were mapped around the two known inhabited patches based on a rough field survey of the vegetation and aerial photos. Altogether, 31 potential habitat patches were surveyed for the presence of the False Ringlet butterfly in June and July 2006; the species' presence was recorded in 16 patches with 12 patches of higher densities. These twelve study patches were isolated from each other by 0.01–3.2 km, separated by softwood forest groves, shrubs, grasslands or agricultural areas (Fig. 1). They varied in size from 0.14 to 1.66 ha. The examined patches were all wet meadows with the ground water level close (0.1–2.0 m) to the surface, and vegetation was dominated by mainly Purple Moorgrass and other Poaceae and *Carex* species with few nectar sources for the butterflies (Örvössy et al. 2010). Forests and shrubs surrounded these meadows. The traditional management of the area was extensive mowing for haymaking. Most of the studied patches had been abandoned without any or with very limited mowing; traditional once a year mowing is still carried out only in three patches (c, d, e on Fig. 1.). The abandoned patches have experienced weed invasion and scrub encroachment.

Sampling

We carried out an extensive mark-release-recapture survey in the twelve habitat patches between the 5th and 28th of June 2007. The butterflies were individually marked using permanent pens on the underside of their hindwings. Each patch was visited every other day. In order to standardize the sampling effort, the duration of each visit depended on the size of the patch; as a standard, the surveyor spent

Fig. 1 The twelve study habitat patches of the False Ringlet metapopulation complex at Ócsa in 2007 using ESRI World Topographic Map
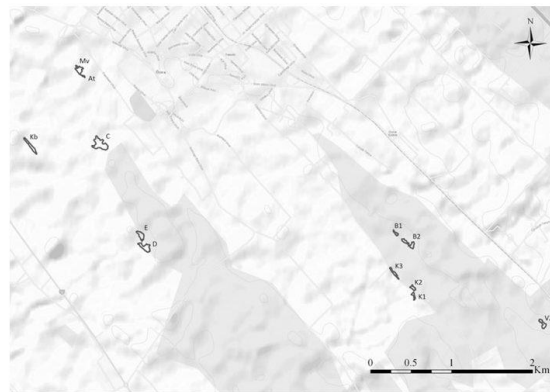
60 min in a 0.5 ha patch. We observed and caught butterflies occasionally (1–3 times) in the four additional locations, these data were included only in the Virtual Migration 2 model (see below), as the model require information about all the known habitat patches. We measured the quality of each habitat patch in randomly distributed 2 × 2 m quadrats (3–7 quadrats per habitat patch depending on their size). Height of vegetation (5 measures per quadrat), height of grass litter (5 measures per quadrat), number of flowers/nectar sources (all flowers of forbs) were measured in all quadrats. The arithmetic mean values of each parameter were used in the analyses. Height of vegetation was measured excluding bushes, from the ground to the surface of grass plants (Poaceae and Carex species mainly). Grass litter was a thick layer of dead leaves, we measured its height from the ground. The thickness of this layer is largely influenced by mowing and hay removal. The area covered by tussocks and percentage of bush cover were estimated for each habitat patch. Area covered by tussocks is a parameter which can be connected to earlier management, as intensive mowing destroys tussock structure (Bartoš et al. 2011). Also tussock structure may have an effect on larval survival by providing hibernating sites in case of high groundwater level. The groundwater level was measured after the flight period by hand-dug wells (5 cm diameter) in each patch. Therefore, the relationship between population size or density of the species and the groundwater level should be treated only as a guideline.

Statistical analysis

The mark-release-recapture dataset was analysed in two steps, and separately for each of the twelve habitat patches. First, we fitted a Cormack–Jolly–Seber (CJS) model to each dataset with time- and sex-dependent parameters (survival rate and recapture probability). We tested for the goodness of fit by a bootstrap GOF test and a χ^2-based GOF test ('Release') (Lebreton et al. 1992). Then we performed a model selection based on AIC values to reach the most parsimonious model (Burnham and Anderson 2002). Secondly, we fitted a Jolly–Seber (JS) model with a set up for survival rate and encounter probability as in the most parsimonious CJS model. Model selection was performed again to find the best parameterization (the JS model had two additional parameters: population size N, which can be sex-dependent, and proportional recruitment $pent$, which can be time- and sex-dependent). Daily population size was a derived parameter of the JS model. Average lifespan was calculated from the survival rate of the CJS model (1/−ln(Phi), Cook et al. 1967). All analyses were carried out using MARK 5.1 software (White and Burnham 1999).

The Virtual Migration 2 programme (Hanski et al. 2000) was used to estimate the following dispersion and population parameters for both sexes: within-patch mortality, migration rate per one-hectare patch, scaling of migration with patch size, distance-dependence of migration, mortality during migration and scaling of immigration into a patch. This programme can handle the problems of different number of dispersal events and capture probability between males and females. Parameter estimation was conducted using 1,000 randomizations in simulated annealing followed by 5,000 intelligent randomizations to converge on the optimum (Hanski et al. 2000). One parameter was fixed, as there were no significant difference between scaling of immigration and scaling of emigration. Confidence intervals for the parameters were estimated based on likelihood ratio tests, we used 2,000 evaluations. Replicate runs were conducted to check for convergence of parameter estimates and confidence intervals.

The relationship between butterfly quantity and habitat quality parameters was analysed with "General Additive Models, for Location, Scale and Shape", without any smoothing effect, only for exploiting the availability of lognormal dispersion. Two response variables were used in the analyses: total population size (the estimated number of all individuals during a flight period in each habitat patch) and the maximum observed density of individuals (observed number of individuals divided by the minutes spent in each habitat patch during the peak day of the flight period). For both dependent variables we fitted a general additive model with lognormal error distribution, without any smoothing effect. Predictor variables were standardized: height of vegetation, height of grass litter, number of flowers/nectar sources, area covered by tussocks, percentage of bush cover, area and groundwater level. We applied a backward-stepwise model selection based on AIC values. These analyses were performed using gamlss package (Stasinopoulos et al. 2012) of R (2.12.2) statistical software (R Development Core Team 2011).

Results

In 2007, due to the hot weather, butterflies emerged earlier than usual; the first observation was on the 3rd of June, the mark-release-recapture was carried out between the 5th and 28th of June. Altogether, 1,496 butterflies (914 males and 582 females) were marked, during 2,052 capture events. The maximum daily butterfly density ranged between 0.09 and 1.72 observed individual per minute per patch, total population size per patch varied between 24 and 1,055 individuals (Table 1). We had sufficient data in ten habitat patches for estimation of the daily population size and survival. The daily survival (SE) varied between 0.22

(0.18) and 0.79 (0.02) for males and 0.82 (0.04) and 0.87 (0.08) for females. The changes in estimated daily population size in the habitat patches are shown in Fig. 2. In all patches protandry was observed, i.e. males emerged earlier than females (Fig. 2). Average lifespan (SE) varied between 0.7 (0.5) and 7.3 (0.3) days (Table 1). The timing of the highest daily population size varied in the ten habitat patches; there were 6 days difference between first and last peaks in the number of individuals. Highest daily population size was observed on the 5th and 6th of June in patch C, D, E, Mv, and between the 10th–12th of June in patch B1, B2, K1, K2, K3, V2. The two groups of patches were separated by relatively large distances and differed in size (Fig. 1). The estimated total number of individuals in the metapopulation was slightly over 3,000, which was calculated for ten habitat patches, where the total estimated number of individuals (SE) varied between 24 (6.7) in patch E and 765 (73.5) males and 290 (28.6) females in patch B2.

As the butterflies were individually marked in twelve patches regularly and in four additional ones occasionally, we had information about the dispersal among habitat patches. Altogether, 48 dispersal events (37 males and 11 females) were detected between habitat patches. Females moved less frequently and shorter distances than males. For males, the longest observed movement was 5.8 km, while the longest observed movement by a female butterfly was less than 0.5 km. The Virtual Migration 2 model showed that one dispersal parameter differed significantly between males and females; distance-dependence of migration was stronger in the case of females (Table 2). The Virtual Migration 2 model's goodness-of-fit test showed that model fit was poor only in two habitat patches (C, V2) for males and in three habitat patches (K1, M, V2) for females (Table 3).

The maximum daily density was significantly affected by the groundwater level and by the area covered by tussocks following the minimal adequate general additive model (Table 4). The density of butterflies was higher in habitats where the groundwater level was lower, and the area covered by tussocks was larger, groundwater level had a stronger effect (Table 4). The depth of groundwater level and the height of grass litter, based on general additive model (Table 4), affected the estimated total population size. The population size was larger in habitat patches where the groundwater level was lower and the grass litter was higher, both parameters had almost equal influence on population size (Table 4).

Discussion

Metapopulation structure

The metapopulation of the False Ringlet at Ócsa, Hungary, is larger both in area and population size than earlier

Table 1 Summary data of the mark-release-recapture dataset, and derived parameters from Cormack–Jolly–Seber model (capture probability, Lifespan) and Jolly–Seber model (total population size)

Habitat patch	Area (ha)	Number of captured individuals		Number of recaptured individuals		Capture probability		Lifespan (SE) (day)		Maximum daily density	Total population size (SE)	
		m	f	m	f	m	f	m	f	Captured individual/ minute	m	f
B1	0.14	46	33	3	4	0.62 (0.76)	0.079 (0.05)	0.7 (0.5)	7.3 (0.4)	0.83	42.0 (<0.1)	93.4 (35.9)
B2	0.53	322	205	79	75	0.15 (0.02)		4.2 (0.3)	7.3 (0.3)	0.95	765.3 (73.5)	289.9 (28.6)
C	1.66	137	82	19	10	0.18 (0.06)		2.8 (0.3)		0.27	384.4 (77.0)	236.3 (49.5)
D	0.79	38	46	5	9	0.34 (0.11)		2.5 (0.4)		0.33	55.9 (12.2)	
E	0.54	16	20	3	5	0.30 (0.13)		3.4 (0.4)		0.17	23.7 (6.7)	
K1	0.16	141	87	19	21	0.19 (0.04)		2.8 (0.3)		1.72	336.8 (53.0)	164.1 (26.6)
K2	0.21	187	128	26	39	0.35 (0.10)	0.16 (0.03)	1.5 (0.4)	5.0 (0.3)	1.42	302.7 (30.9)	
K3	0.27	115	65	24	22	0.17 (0.03)		4.2 (0.3)		0.78	225.7 (33.1)	114.4 (19.3)
M	0.53	85	54	24	12	0.27 (0.06)		4.0 (0.3)		0.48	102.7 (7.4)	
V2	0.42	89	110	39	52	0.30 (0.04)	3.7 (0.3)	6.9 (0.3)		0.46	94.4 (7.4)	
At	0.04	7	3	4	0					0.60		
Kb	0.57	7	10	5	0					0.09		

Here we present the most parsimonious models, in some cases gender differences appeared in parameter values (m: male, f: female). The Cormack-Jolly-Seber models were for each patches: B1, K2 [*Phi*(g), *P*(g)]; B2, V2 *Phi*(g),*P*()]; C, D, E, K1, K3, Mv [*Phi*(),*P*()]. The number of marked and recaptured butterflies was not large enough for model parameter estimation with Cormack–Jolly–Seber nor with Jolly–Seber method in patch At and Kb. The Jolly–Seber model did not fit for males of patch B1, due to low recapture rate
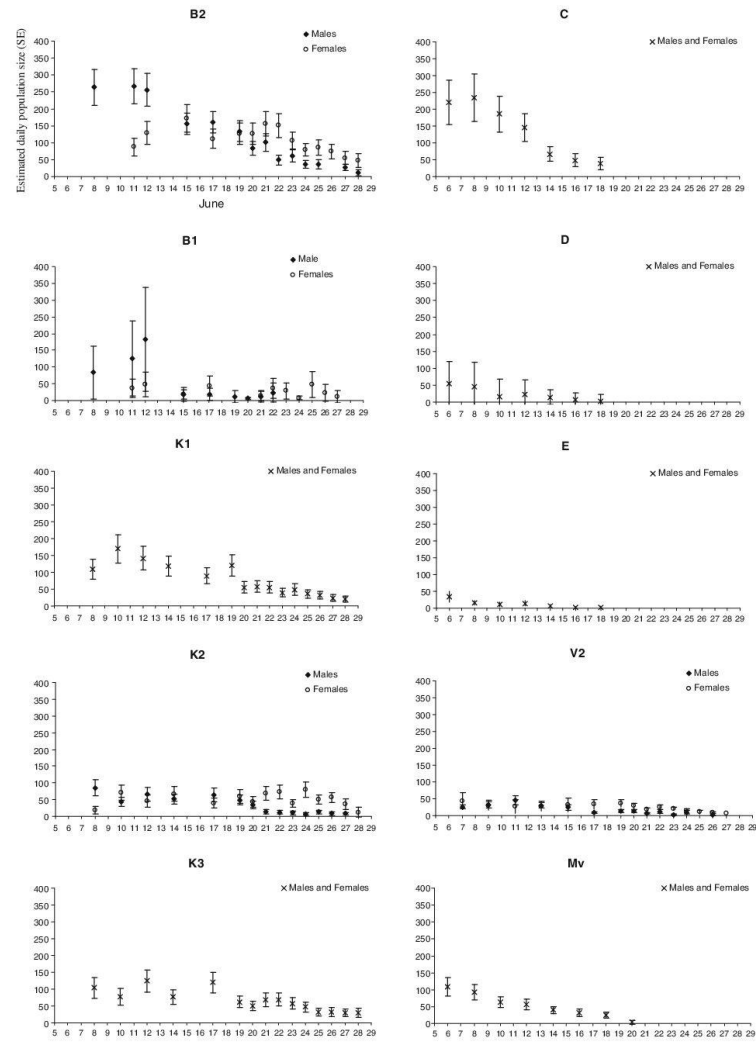
◀ **Fig. 2** Estimated daily population sizes (±SE). Estimation was based on MRR dataset analysis with a Jolly-Seber model. The best model was gender dependent in patch B1, B2, K2 and V2, hence males and females are illustrated separately, while in the other patches estimated daily population sizes were illustrated jointly for males and females. The Jolly-Seber model did not correctly fit for males of patch B1, therefore SE values are large

Table 2 Parameter estimates from the Virtual Migration 2 model (95 % confidence intervals in parentheses) for False Ringlet within the 12 study and 4 additional meadow patches

	Male parameter value	Female parameter value
Within-patch mortality	0.096 (0.000; 0.231)	0.112 (0.000; 0.180)
Emigration constant	0.140 (0.032; 0.266)	0.071 (0.011; 0.201)
Scaling of emigration	−0.189 (−0.463; −0.000)	−0.000 (−0.545; 0.000)
Distance dependence	**1.026 (0.654; 1.554)**	**0.210 (0.000; 0.625)**
Migration mortality	3.896 (0.000; 8.239)	14.546 (0.000; 58.531)
Scaling of immigration	–	–

Distance dependence differed significantly between males and females. Significant differences between sexes are shown in bold. Scaling of emigration and immigration did not differ significantly; therefore, scaling of immigration was a fixed parameter

estimations suggested (Bálint and Máté 2004), but it is divided into small subpopulations. This indicates that the population complex may be vulnerable due to small sub-population sizes. Spatial isolation of the subpopulations raises the possibility of a metapopulation structure. The attributes of classic metapopulations include colonization-extinction dynamics, fast turnover rate, sufficient dispersal among habitat patches, asynchronous dynamics of the local populations, and strict distinction between habitat and hostile matrix (Hanski and Glipin 1997; Hanski 1998; Bourn et al. 2000). Our results suggest that female dispersal is very low, hence, probability of recolonization is low, and a fast turnover rate is unlikely (Hanski and Glipin 1997). While females move only among the closest habitats, there is evidence that males are able to move between all the examined habitat patches. Similar gender differences in dispersal were also observed in an Italian population (Bonelli et al. 2010). In a Slovenian habitat complex the maximum observed dispersal movement was less than 340 m (Čelik and Verovnik 2010), whereas a Croatian study shows no dispersal even among close habitat patches (<450 m; Šašić 2010).

Spatial asynchrony in demography of local populations can also be frequently detected in metapopulation dynamics (Sutcliffe et al. 1997). In the studied metapopulation, there were two groups of habitat patches with 6 days difference between the peaks of the estimated daily

Table 3 Virtual Migration 2 model goodness-of-fit test for each habitat patch separately for males and females

Habitat	Males						Females					
	Residents		Emigrants		Imigrants		Residents		Emigrants		Imigrants	
	Q	df	Q	df	Q	df	Q	df	Q	df	Q	df
B1	0.44	23	0.12	11	0.28	11	0.32	22	0.03	11	0.11	10
B2	1.36	23	0.54	11	0.28	11	0.41	22	0.23	11	0.10	10
C	**1,418.37**	13	**1,418.36**	6	0.01	6	0.04	13	0.03	6	0.02	6
D	0.03	13	0.01	6	0.02	6	0.03	13	0.02	6	0.01	6
E	0.01	13	0.01	6	0.01	6	0.02	13	0.01	6	0.01	6
K1	2.17	23	0.23	11	0.15	11	**34.32**	22	0.10	11	32.51	10
K2	0.72	23	0.20	11	0.19	11	32.95	22	32.54	11	0.11	10
K3	0.77	23	0.17	11	0.19	11	1.66	22	0.07	11	0.12	10
M	0.01	13	0.00	6	0.01	6	**208.29**	13	**208.27**	6	0.02	6
V2	**1,422.41**	23	0.06	11	**1,418.55**	11	**213.90**	23	0.10	11	**208.37**	11
At	0.01	13	0.00	6	0.01	6	0.01	8	0.00	1	0.01	1
Kb	0.00	13	0.00	6	0.01	6	0.02	13	0.00	6	0.01	6
A	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
Bt	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
S	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
V1	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0

Significant ($p > 0.05$) lack of fit are shown in bold

Table 4 Results of general additive model analyses showing the minimal adequate models for maximum density and total population size of the False Ringlet

Dependent variable	AIC of basic model with intercept only	AIC of lowest AIC model	Explanatory variables	Parameter estimates (SE)
Maximum density	17.03	−1.21	Groundwater level	**0.67 (0.09)**
			Area covered with tussocks	**0.39 (0.09)**
Total population size	143.00	131.86	Groundwater level	**0.59 (0.14)**
			Height of grass litter	**0.66 (0.15)**

Groundwater level, area covered by tussocks and height of grass litter are significantly related with the density and total population size of False Ringlet

Significance of estimated parameters in all cases: $p < 0.001$

population sizes. The first peak occurred in the largest, more open patches on the western side of the study area, while the latest peak was in the smaller, more closed habitat patches on the eastern side (Fig. 2.). In this case, the distance between the two groups and difference between habitat characteristics (such as area and shading) may together have caused the asynchrony among subpopulations. This asynchrony is probably not large enough to save a subpopulation from environmental perturbations, such as unfavourable weather conditions, but can strengthen the metapopulation, as the two groups of patches are separated by time and distance. Dispersal among habitat patches is possible, as patches inhabited by the metapopulation have soft rather than sharp habitat boundaries. Several male butterflies were spotted in between habitat patches, indicating that the matrix is suitable for longer persistence, although, female dispersal is more limited. These differences in dispersal distances may be a result of sex-specific effects of unfavourable matrix environment on flight speed, as was shown by Turlure et al. (2011) in *Boloria* butterflies. Dispersal was not even among patches, and the VM2 model did not fit in some patches. Those patches probably differed in habitat quality, affecting dispersal pressure (Baguette et al. 2011).

According to these results, the metapopulation of False Ringlet at Ócsa is consisted of two groups of habitat patches that can aid the long-term survival of each other, although we did not observe any female dispersal between the two groups. Female dispersal was limited to very short distances, but male dispersal might have been also controlled by habitat quality, alongside patch area and distance. Our results indicate that creating stepping-stones or corridors for females between habitat patches may have a positive effect on female dispersal and therefore strengthen the metapopulation. Although, to reveal the metapopulation structure, the long-term study of patch occupancy and local population asynchrony is necessary, while a genetic study would help to assess the present and past possibilities of dispersal.

Habitat quality, requirements and management

Habitat patches differed in several ways, in area, quality and earlier and current management. Patches in the same size were very different in the number of marked individuals (Table 1). Habitat patch B2 has a large subpopulation versus patch E or Kb. While the small number of marked individuals in patch Kb can be explained by its distance from the core habitat patches, the centrally located patch E must be of lower quality as it only supports a small population. In addition, there are differences in the lifespan of males and females among the habitat patches. Lifespan is calculated from apparent survival probability, which is negatively related with dispersal from a given patch. Greater dispersal can be caused by several factors, including lower habitat quality, males searching for female and density dependent dispersal (Baguette et al. 2011). In this case, male butterflies in patch B1 have a very short estimated lifespan, which is probably a result of a combination of poor model fitting and a high emigration rate, and not a locally high death rate. A high emigration rate of males in this patch may be the result of a low number of females in that patch. Overall, male dispersal was greater than female dispersal, explaining the lower apparent survival and so shorter lifespan of males. The shorter estimated lifespan, compared to other studies (Čelik and Verovnik 2010; Örvössy et al. 2010) is probably the consequence of dispersal among local habitat patches.

Determination of habitat quality in the patches and the requirements of the species can help determine proper habitat management, which can facilitate long-term persistence of the subpopulations. Three variables of habitat quality were of particular importance: groundwater level, height of grass litter and the area covered by tussocks. Our expectation was that higher water level increases habitat quality for the subpopulations, as the species lives in wet meadows and the local and several other European populations are suffering from the effects of land drainage (Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010;

Sielezniew et al. 2010). In contrast to this, we found that the patches with lower groundwater level were inhabited by larger and denser subpopulations. However, we have to acknowledge that this phenomenon is only true at this range of groundwater level, as the surrounding unoccupied drier uninhabited areas were not included in the study. In the light of the fact that there are plans to increase the groundwater level in the area, this is an especially important result. The groundwater level may have a detrimental negative effect on larval survival by changing vegetation structure and microclimate. Rapid and drastic increases of groundwater level should be avoided, as this could destroy the habitat as well as the population. An earlier study on *Coenonympha tullia* showed that larvae can climb up to high positions during flooding (Joy and Pullin 1996). Therefore maintaining tall vegetation is important for larval survival in areas subject to flooding. During winter and early spring the area can be covered by water and the existence of dry areas can be crucial for the survival of larvae. Adult False Ringlet butterflies locally may prefer semi-open habitats with bushes (Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010), because bushes develop well where the groundwater is not so high and provide a better microclimate for the butterflies in hot summers. More specifically, the groundwater level should be high enough to maintain the *Molinietum* vegetation for the species, but sufficiently low to allow larval survival and the presence of bushes for adult preferences.

Although the presence of bushes might increase the size and density of subpopulations, encroachment of bushes due to abandonment of these wet meadows can destroy the habitats in the study area and in other European locations as well (Bräu et al. 2010; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010). Regular mowing can prevent the spread of weeds, such as *Solidago* spp. and encroachment of bushes, but also has a negative effect on tussock structure and amount of grass litter (Bartoš et al. 2011).

Structured vegetation with tussocks and large amounts of grass litter were among the most important factors affecting population density and size in the study area. The maximum daily density was higher in habitat patches where tussocks covered a large proportion of the patch, and the estimated population size increased with the height of grass litter. This could be the consequence of larvae overwintering inside the tussocks and grass litter (Bräu et al. 2010). Traditionally, infrequent (once yearly) mowing by hand in autumn maintained these semi open meadows. Too frequent mowing could lead to the loss of grass litter and of tussock structures, while lack of mowing would result in the overgrowing of the area (Skórka et al. 2007). For future prospects, a mowing experiment would help to reveal what kind of management can maintain an optimal habitat quality. Before that, there is an urgent topic to examine. The water level is going to be increased on the area to halt decades of slow desiccation. This process will rearrange the metapopulation structure: patch location, habitat size and quality, dispersal possibilities etc. Following this process would answer some questions about how this metapopulation reacts to habitat changes and its precise structure.

References

Aistleitner U, Mayr T, Siegel C (2006) Nachweise von neuen, verschollenen und stark gefahrdeten Grosschmetterlingen aus Vorarlberg, Austria occ. (Lepidoptera). Z Arb Gem Ost Ent 58:1–10

Baguette M, Nève G (1994) Adult movements between populations on the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). Ecol Entomol 19:1–5

Baguette M, Clobert J, Schtickzelle N (2011) Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. Ecography 34:170–176

Bálint Z, Máté A (2004) Ezüstsávos szénalepke (*Coenonympha oedippus*) fajmegőrzési terv. [False ringlet (*Coenonympha oedippus*) species conservation actionplan.] KvVM Természetvédelmi Hivatala, Budapest

Bartoš M, Janeček S, Klimešová J (2011) Effect of mowing and fertilization on biomass and carbohydrate reserves of Molinia caerulea at two organizational levels. Acta Oecol 37:299–306

Bonelli S, Canterino S, Balletto E (2010) Ecology of *Coenonympha oedippus* (Fabricius, 1787) (Lepidoptera: Nymphalidae) in Italy. Oedippus 26:25–30

Bourn NAD, Pearman GS, Goodger B, Thomas JA, Warren MS (2000) Changes in the status of two endangered butterflies over two decades and the influence of grazing management. In: Rook AJ, Penning PD (eds) Grazing management. British Grassland Society, Reading, pp 141–146

Bozano GC (2002) Guide to the butterflies of the Palearctic region. Satyrinae part III. Omnes Artes, Milano

Bräu M, Dolek M, Stettmer C (2010) Habitat requirements, larval development and food preferences of the German population of the False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae)—research on the ecological needs to develop management tools. Oedippus 26:41–51

Burnham KP, Anderson DR (2002) Model selection and multi-model inference. A practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Čelik T (2004) Population dynamics of endangered species *Coenonympha oedippus* Fabricius, 1787 (Lepidoptera:Satyridae) on the Ljubljansko Baarje (Slovenia). Acta Entomol Slovenica 12:99–114

Čelik T, Verovnik R (2010) *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Slovenia. Oedippus 26:7–15

Čelik T, Vreš B, Seliškar A (2009) Determinants of within-patch microdistribution and movements of endangered butterfly *Coenonympha oedippus* (Fabricius, 1787) (Nymphalidae: Satyrinae). Hacquetia 8:115–128

Cook LM, Brower LP, Croze HJ (1967) The accuracy from a population estimation from multiple recapture data. J Anim Ecol 36:57–60

Dennis RLH, Shreeve TG, Van Dyck H (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodivers Conserv 15:1943–1966

Dover J, Settele J (2009) The influence of landscape structure on butterfly distribution and movement: a review. J Insect Conserv 13:3–27

Dušej G, Wermeille E, Carron G, Ziegler H (2010) Concerning the situation of the False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Switzerland. Oedippus 26:38–40

Erhardt A, Thomas JA (1991) Lepidoptera as indicators of change in the seminatural grasslands of lowland and upland Europe. In: Collins NM, Thomas JA (eds) The conservation of insects and their habitats. Academic Press, London, pp 213–237

Fischer K, Beinlich B, Plachter H (1999) Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. J Insect Conserv 3:43–52

Gorbunov P (2001) The butterflies of Russia: classification, genitalia, keys for identification (Lepidoptera: Hesperioidea and Papilionoidea). Dissertation, Russian Academy of Sciences, Institute of Plant and Animal Ecology

Gorbunov P, Kosterin O (2007) The butterflies (Hesperioidea and Papilionoidea) of North Asia (Asian part of Russia) in nature. Rodina and Fodio, Moscow

Halada L, Evans D, Romão C, Petersen J (2011) Which habitats of European importance depend on agricultural practices? Biodivers Conserv 20:2365–2378. doi:10.1007/s10531-011-9989-z

Hambler C, Henderson PA, Speight MA (2011) Extinction rates, extinction-prone habitats, and indicator groups in Britain and at larger scales. Biol Conserv 144:713–721

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I (2003) Biology of extinctions in butterfly metapopulations. In: Boggs CL, Watt WB, Ehrlich PR (eds) Butterflies: ecology and evolution taking flight. University of Chicago Press, Chicago, pp 577–602

Hanski I, Gilpin ME (1997) Metapopulation biology. Ecology, genetics and evolution. Academic Press, San Diego

Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81:239–251

Hovestadt T, Binzenhofer B, Nowicki P, Settele J (2011) Do all inter-patch movements represent dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. J Anim Ecol 80:1070–1077

IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Accessed 15 November 2011

Joy J, Pullin AS (1996) The effects of flooding on the survival and behaviour of overwintering large heath butterfly *Coenonympha tullia* larvae. Biol Conserv 82:61–66

Kučinić M, Tvrtković N, Kletečki E (1999) The False Ringlet is a member of the Croatian butterfly fauna after all. Nat Croat 8:399–404

Kudma O (2002) The distribution atlas of European butterflies. Oedippus 20:1–343

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Lenda M, Skórka P (2010) Patch occupancy, number of individuals and population density of the Marbled White in a changing agricultural landscape. Acta Oecol 36:497–506

Lhonoré J, Lagarde M (1999) Biogeographie, ecologie et protection de *Coenonympha oedippus* (Fab., 1787) (Lepidoptera: Nymphalidae: Satyrinae). Ann Soc Entomol France 35:299–307

Nowicki P, Pepkowska A, Kudlek J, Skórka P, Witek M, Settele J, Woyciechowski M (2007) From metapopulation theory to conservation recommendations: lessons from spatial occurrence and abundance patterns of *Maculinea* butterflies. Biol Conserv 140:119–129

Öckinger E (2006) Possible metapopulation structure of the threatened butterfly *Pyrgus armoricanus* in Sweden. J Insect Conserv 10:43–51

Oostermeijer JGB, van Swaay CAM (1998) The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biol Conserv 86:271–280

Örvössy N, Vozár Á, Kőrösi Á, Batáry P, Peregovits L (2010) Structure and size of a threatened population of the False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Hungary. Oedippus 26:31–37

Parmesan C (2003) Butterflies as bioindicators for climate change effects. In: Boggs CL, Watt WB, Ehrlich PR (eds) Butterflies: ecology and evolution taking flight. University of Chicago Press, Chicago, pp 541–560

Rabasa SG, Gutiérrez D, Escudero A (2008) Relative importance of host plant patch geometry and habitat quality on the patterns of occupancy, extinction and density of the monophagous butterfly *Iolana iolas*. Oecologia 156:491–503

Sanford MP, Dennis DM, Brussard PF (2011) Distinguishing habitat types and the relative influences of environmental factors on patch occupancy for a butterfly metapopulation. J Insect Conserv. doi:10.1007/s10841-011-9376-9

Šašić M (2010) False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Croatia: current status, population dynamics and conservation management. Oedippus 26:16–19

Sawchik J, Dufrêne M, Lebrun P (2003) Estimation of habitat quality based on plant community, and effects of isolation in a network of butterfly habitat patches. Acta Oecol 24:25–33

Sielezniew M, Pałka K, Michalczuk W, Bystrowski C, Hołowiński M, Czerwiński M (2010) False Ringlet *Coenonympha oedippus* (FABRICIUS, 1787) (Lepidoptera: Nymphalidae) in Poland: state of knowledge and conservation prospects. Oedippus 26:20–24

Skórka P, Settele J, Woyciechowski M (2007) Effects of management cessation on grassland butterflies in southern Poland. Agric Ecosyst Environ 121:319–324

Stasinopoulos M, Rigby B, Akantziliotou C (2012) Instructions on how to use the gamlsss package in R. http://www.gamlss.org/images/stories/papers/gamlss-manual.pdf. Accessed 03 August 2012

Staub R, Aistleitner U (2006): Das Moor-Wiesenvögelschen (*Coenonympha oedippus*)—oder worauf es im grenzüberschreitenden Artenschutz ankommt. In: Broggi MF (ed) Alpenrheintal—eine Region im Umbau. Analysen und Perspektiven der räumlichen Entwicklung, Verlag der Liechtensteinischen Akademischen Gesellschaft, Schaan, pp 245–254

Sutcliffe OL, Thomas CD, Yates TJ, Greatorex-Davies JN (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. Oecologia 109:235–241

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Thomas JA (1991) Rare species conservation: case studies of European butterflies. In: Spellerberg I, Goldsmith B, Morris MG (eds) The scientific management of temperate communities for conservation. Blackwell, Oxford, pp 149–197

Thomas CD, Hanski I (1997) Butterfly metapopulations. In: Hanski I, Gilpin ME (eds) Metapopulation biology, ecology, genetics and evolution. Academic Press, San Diego, pp 359–386

Thomas JA, Morris MG (1994) Patterns, mechanisms and rates of decline among UK invertebrates. Philos Trans R Soc Lond B 344:47–54

Thomas JA, Clarke RT, Elmes GW, Hochberg ME (1998) Population dynamics in the genus Maculinea. In: Dempster JP, McLean IFG (eds) Insect population dynamics: in theory and practice. Chapman & Hall, London, pp 261–290

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc R Soc Lond B 268: 1791–1796

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881

Turlure C, Baguette M, Stevens VM, Maes D (2011) Species- and sex-specific adjustments of movement behavior to landscape heterogeneity in butterflies. Behav Ecol 22:967–975

van Halder I, Barbaro L, Corcket E, Jactel H (2008) Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodivers Conserv 17:1149–1169

van Swaay CAM (2002) The importance of calcareous grasslands for butterflies in Europe. Biol Conserv 104:315–318

van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren M, Wiemers M, Wynhoff I (2010) European red list of butterflies. Publications Office of the European Union, Luxembourg

Vanreusel W, Van Dyck H (2007) When functional habitat does not match vegetation types: a resource-based approach to map butterfly habitat. Biol Conserv 135:202–211

van Swaay CAM, Warren MS (1999) Red Data book of European butterflies (Rhopalocera). Nature and Environment, No. 99, Council of Europe Publishing, Strasbourg, pp 260

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138

HABITAT REQUIREMENTS OF THE PROTECTED
SOUTHERN FESTOON (*ZERYNTHIA POLYXENA*);
ADULT, EGG AND LARVAL DISTRIBUTION
IN A HIGHLY DEGRADED HABITAT COMPLEX

Noémi Örvössy[a], Ádám Kőrösi[b,c], Péter Batáry[d], Ágnes Vozár[e] and László Peregovits[f]

[a]*Institute of Ecology and Botany, MTA Centre for Ecological Research
H-2163 Vácrátót, Alkotmány u. 2–4, Hungary; E-mail: orvossyn@gmail.com*
[b]*MTA–ELTE–MTM Ecology Research Group
H-1117 Budapest, Pázmány Péter s. 1/c, Hungary*
[c]*Field Station Fabrikschleichach, Biocenter, University of Würzburg
Glasshüttenstr. 5, 96181 Rauhenebrach, Germany*
[d]*Agroecology, Georg-August University, Waldweg 26, D-37073 Göttingen, Germany*
[e]*Ministry of Environment and Water, State Secretariat for Nature and Environment Protection,
H-1011 Budapest, Fő u. 44-50, Hungary*
[f]*Pars Ltd, H-2094 Nagykovácsi, Rózsa u. 17, Hungary*

Habitat quality affects the presence and size of butterfly populations. Resources for all life stages must be found in a given or few habitat patches. Southern festoon (*Zerynthia polyxena*) is a vulnerable, but locally abundant species in Hungary. The larva requires birthwort (*Aristolochia clematitis*) as food plant. We examined the small scale habitat use of adults and distribution of eggs and larvae among different vegetation types to reveal the requirements of the species in all life stages. Transect counts were conducted in a tree plantation complex comprising four types of vegetation. Number (±SE) of adults, eggs and larva were lowest in poplar plantation (adult 0.3±0.2, egg 1.1±1.1, larva 0.6±0.3). Medium amount of butterflies were observed in open (adult 8.3±2.9, egg 3.1±2.6, larva 3.1±1.9) and black-locust (adult 9.4±4.2, egg 12.7±4.9, larva 4.1±1.1) habitat. Number of butterflies was highest in hummocks (adult 13.5±1.5, egg 12.9±5.7, larva 8.4±2.1). Adults avoided bare ground. We encountered most eggs in dense food plant patches with high plants. Food plant height also positively influenced the occurrence of the larvae. Although distribution of adults and juvenile forms showed quite similar patterns, we could also reveal some differences that caused by different environmental conditions in distinct vegetation types. Our study stresses the importance of habitat quality, which affects population size of butterflies even in a highly degraded habitat complex.

Keywords: habitat quality, habitat patch, life stage, resource use, tree plantations.

INTRODUCTION

The occurrence of a butterfly species can be significantly affected by the area, isolation and quality of the habitat (Thomas *et al.* 1992, Wahlberg *et al.* 2002). While some investigations considered patch geometry as the most relevant factor (Hanski *et al.* 1996, Thomas & Hanski 1997, Nowicki *et al.* 2007), other studies revealed that within-site variation in habitat quality is more important in predicting patterns of site occupancy (Thomas *et al.* 2001, Fleish-

MAN *et al.* 2002). Most ecological studies examining the role of habitat quality, area and isolation in butterfly occurrence and abundance pattern face the problem of habitat definition. Although defining a habitat patch is essential in these studies, adequate definition can be difficult, especially in continuous landscapes in which landscape elements do not help to identify suitable habitats. In the course of habitat definition specific requirements of all life stages should be considered, since different life stages use different resources and all of them should be found within reach. Habitats may consist of different vegetation patches, containing one or more resources for the species, but not necessarily all of them at once. In light of the fact that such resources at finer spatial scale do not necessarily overlap in the area occupied by the butterfly, determining the habitat patch solely on the basis of the presence of the food plant is not always appropriate (DENNIS *et al.* 2006).

In continuous landscapes, in which spatial limitation and isolation has little effect on the distribution of a given species, significance of habitat quality is relatively more important. Habitat quality can be described by structural factors, such as the amount of shade or light intensity (GRUNDEL *et al.* 1998), by main components of vegetation and food plant density (BATÁRY *et al.* 2007), or by the prevalence of sources of nectar, which can influence the density of adults within a suitable habitat (FISCHER 1998). Females and males can have different habitat requirements due to their different drives, such as finding suitable sites for oviposition or mating partners (BULL *et al.* 1985, MUNGUIRA *et al.* 1997, GRUNDEL *et al.* 1998). For some butterfly species, habitat permanence is also an important component of habitat quality (FISCHER *et. al.* 1998), while other species are adapted to changing environments (WARREN 1987). Vegetation management can also influence the quality of habitats, and therefore the habitat use of butterflies (SMALLIDGE & DONALD 1997).

Habitat quality requirements can be different for the given life stages, as they require different resources (DENNIS *et al.* 2006). The distribution and density of adult butterflies itself are not necessarily good predictors of oviposition sites (DOVER & ROWLINGSON 2005), because habitat requirements of eggs and larvae are usually narrower than those of the adults, therefore these stages determine essentially the distribution of butterfly species (THOMAS 1991, ELLIS 2003). Females try to choose the most appropriate places for egg laying. Oviposition sites may be chosen on the basis of structural parameters such as distance from the habitat edge (BERGMAN 1999), light intensity (MEYER & SISK 2001), fundamental rock (THOMAS 1983), area of bare ground (THOMAS *et al.* 1986), soil cover (FISCHER *et al.* 1998) or structure of shade (GRUNDEL *et al.* 1998). Food plant features, such as size and abundance, thickness of food-plant leaves' mesophyllum and organic nitrogen content are also important factors affecting the choice of oviposition site (BOURN & THOMAS 1993, ELLIS 2003). Other, non-food plant characteristics can also affect the selection of

oviposition site, e.g., sward height (Thomas 1983, Thomas *et al.* 1986, Ellis 2003). Microhabitat features can have a considerable effect on larval survival, as demonstrated e.g., in the case of *Coenonympha tullia* (Sei & Porter 2003). Occurrence of *Euphydryas aurinia* larvae associated with high food plant cover and short grasses (Konvička *et al.* 2003).

Our aims were to determine factors affecting the small-scale habitat use of southern festoon (*Zerynthia polyxena*), including the use of food plant patches by adults and the distribution of eggs and larvae among food plant patches, and to reveal the resource requirements of the species in all life stages in a human-dominated landscape. We studied a population inhabiting a tree plantation habitat complex where food plant patches of various size and density occurred in four different vegetation types: poplar plantation, black-locust (*Robinia pseudo-acacia*) plantation, hummocks created by stubbings and clearings. We hypothesized that structural differences of food plant patches in different vegetation types has an effect on distribution and abundance of the southern festoon.

MATERIAL AND METHODS

The southern festoon (*Zerynthia polyxena* [Denis et Schiffermüller], 1775) is a papilionid butterfly distributed from Central and South Europe to the Southern Ural Mts. The northern edge of its range is in the Carpathian Basin, where the species occupies disturbed habitats with nitrogen-rich soil such as gallery forests, abandoned orchards and vineyards, clearings, poplar and black locust plantations and roadsides. The agricultural intensification, river control and urbanization caused a decline in natural disturbance of such habitats in Europe (Smallidge & Leopold 1997), thus butterflies requiring disturbed habitats have been forced to use human-dominated and artificially disturbed habitats (Robertson *et al.* 1995). Today most populations of the southern festoon can be found in black locust plantations, road verges, riparian woodlands and degraded deciduous forests (Bálint *et al.* 2006). In plantations, due to forestry management, the disturbed, nitrogen-rich soil provides excellent conditions for the food plant of the caterpillars.

The flight period is between late April and early June. Caterpillars hatch a week after the oviposition and pupate in July. In the study area the flight period started on the 26th of April in 2005. This species is oligophagous, but in Hungary its larval food plant is exclusively the birthworth (*Aristolochia clematitis*).

Study area

The population studied lives in a poplar (*Populus × euramericana*) plantation mixed with black-locust (*Robinia pseudo-acacia*) patches near Csévharaszt on the Hungarian Great Plain (47°18′59″N, 19°26′18″E). Four vegetation types were available for the butterflies: poplar- and black-locust plantations, hummocks and clearings. Hummocks created by the forestry during the earlier deforestation built-up from stumps of harvested trees merged to a 1.5–2 m high, narrow (~8 m) and long (~200 m) belt covered with soil. These structures were partly shaded and disturbed, which is ideal for birthworth. The larval food plant

was present in all type of vegetation, but in different quantity. Before the butterfly survey (between 3rd and 6th of May), a map of food plant patches of the study area was prepared with *ca.* 2-m precision using GPS Trimble GeoExplorer3 (Trimble Navigation Ltd., USA) (Fig. 1). Food plants appeared some days later than the start of the flight period in the study year. Transects were designated during the following days. In every available habitat type unit a transect was designated, so that each transect was inside in a distinct food plant patch. Each clump of food plants in which the density of shoots was at least five shoot per m² and which was separated by at least 10 m from other clumps, was considered a distinct patch. The mean food plant patch size was 1966 m² (SEM 450).

Study design and sampling

Altogether 23 large food plant patches were selected for sampling (Fig. 1). Each patch was located in one of the four vegetation types: 6 in poplar plantation, 7 in black-locust plantation, 6 in hummocks and 4 in clearings. To avoid pseudo-replication in each separated habitat type unit only one transect was designated. Transects (6 × 40 m) starting point and direction were selected randomly in every food plant patch. Each transect was divided into 4 m long and 1 m wide plots, and every second plot (altogether five plots per transect) was used for egg and larva census and vegetation survey.

Number of adults was counted twice a day at each transect, altogether 16 times, between May 13–26, 2005. Transects were visited in altered order to avoid effects of timing. Number of eggs and larvae was counted twice in each plot, at the first in the middle of the flight period in 11th–12th of May and the second time at 31st of May. Number and height of food plants, height of other plants and percentage of bare ground were measured at the
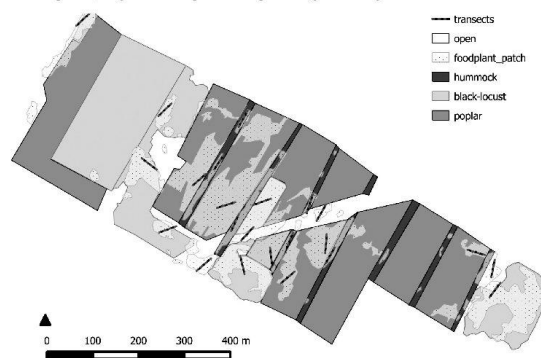

Fig. 1. Habitat map of the study area at Csévharaszt, Central Hungary.

same time. Light intensity was measured on each transect during the second survey by a photometer (LI-189 Quantum/Radiometer/Photometer) at 100 points 120 cm above the ground between 12:00 noon and 1:00 p.m.

Transects and sampling plots covered only a smaller part of a larger habitat complex, but the large density of adults, eggs and larvae made this possible. Sampling area upper limit was the necessary separation of transects to avoid semi-replication, while labour and time effort limited the frequency of egg and larval censuses.

Statistical analyses

Due to the overdispersion and heteroscedasticity in our dataset, and correlations among explanatory variables, we used conditional inference trees to analyse our data. Tree based methods are getting more popular in life sciences, but relatively new to field ecology (Low *et al.* 2006). This method is a variant of 'recursive binary partitioning' or 'trees', a class of simple regression models for prediction and explanation (Hothorn *et. al* 2006). It is a powerful and easy to understand statistical method, which can substitute regression models and produce similar or better results without the strict restrictions of parametric regression models (Hothorn *et. al* 2006). Nagy *et al.* (2010) showed the advantage of conditional inference tree method in a comparative study of two tree based methods and a regression method.

Generally, tree-based methods split the sample step by step into smaller and smaller groups according to mathematical conditions. Conditional inference tree uses regression estimation for splitting the sample into two groups at each node. The recursive binary partitioning is embedded into a well-defined framework of conditional inference procedures, hence both the overfitting, and variable selection problem induced by a recursive fitting procedure are solved (Hothorn *et. al* 2006). If the outcome variable is measured on a continuous scale (as in the present study), the method is called regression tree whereas in case of a categorical outcome variable it is called classification tree (Nagy *et al.* 2010).

We carried out six regression tree analyses with quad type test statistic and Bonferroni correction. Number of adults, eggs and larvae as response variables were analysed separately. In the first three trees explanatory variable was only the vegetation category, while in the other three trees we used undergrowth parameters as explanatory variables: height of food plants, number of food plants, height of other undergrowth plants, percentage of bare ground and (only in the case of adults) light intensity. The separation of vegetation category and undergrowth parameters was necessary as vegetation type clearly influenced the undergrowth parameters (see Results). Conditional inference trees are not sensitive to the association between explanatory parameters, as the hierarchy of the outcome can show the connection among them. We also included the transect ID that each plot belonged to. We used the data of the first undergrowth survey in the case of eggs, because in that instance only 5.7% of the offspring were in the larval stage, and used the second survey in the case of larvae, when only 4.6% were still in egg stage. In the case of eggs another conditional inference tree was made, where presence or absence of eggs in a plot was the dependent variable. Undergrowth parameters by vegetation type were tested by Kruskal-Wallis test, and Multiple Comparison after Kruskal-Wallis test. Correlations of the undergrowth parameters with light intensity were tested by Spearman correlation tests. We used R 3.1.0 for statistical analysis (R Development Core Team 2014); the 'party' package was used for conditional inference tree analysis (Hothorn *et. al* 2006), the pgirmess (Giraudoux 2014) package was used for Multiple Comparison after Kruskal-Wallis test.

Table 1. Adult, egg and larva distribution in the four vegetation types.

	Adult (SE)	Egg (SE)	Larva (SE)
Poplar	0.3 (0.2)	1.1 (1.1)	0.6 (0.3)
Open	8.3 (2.9)	3.0 (2.6)	3.1 (1.9)
Black-locust	9.4 (4.2)	12.7 (4.9)	4.1 (1.1)
Hummock	13.5 (1.5)	12.9 (5.7)	8.4 (2.1)

RESULTS

Altogether 182 butterflies were observed over the course of 16 sampling occasions along the 23 transects. Southern festoon adults used the food plant patches in all of the four vegetation types, but their distribution was uneven (Table 1, Fig. 2). Number of adults was significantly lower in poplar plantations than in other types. Number of butterflies was significantly higher in transects with smaller percentage of bare ground. In transects where bare ground cover was >25%, number of food plants had a nearly significant positive effect on butterfly numbers (Fig. 3).

922 eggs were counted just after the peak of the flight period. Eggs were present in 28 out of the 115 sampling plots (14 hummock, 11 black-locust, 2 open, 1 poplar plots). Number of eggs was only marginally significantly higher in black locust and hummock plots than in open and poplar plots (Fig. 3). The result of 'conditional inference tree' analysis with the undergrowth parameters as explanatory variables showed, that the first node of the tree was host plant height (Table 3). Plots with higher than 45 cm host plants host-
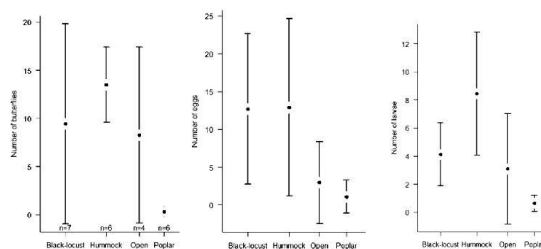
Fig. 2. Mean number of adults, eggs and larvae in the four vegetation types. Bars indicate 95% confidence intervals.

Table 2. Habitat characteristics of the four vegetation types examined during the first (1) and second (2) survey. Mean (±SE) number and height of food plants and mean (±SE) percentage of bare ground cover per plots in each type of vegetation and mean (±SE) light intensity/each transects in the four vegetation category.

|	height of food plants (cm)		number of food plants		% cover of bare ground		height under-growth (cm)		light intensity (lux)
	1	2	1	1	2	2	1	2	2
Poplar	31.4 ±4.4	55.0 ±7.5	29.0 ±1.6	63.4 ±1.5	43.8 ±4.9	49.7 ±2.7	29.4 ±1.9	32.8 ±1.7	412.8 ±66.0
Open	53.8 ±9.2	149.5 ±15.1	23.5 ±1.6	17.7 ±2.9	4.5 ±1.1	51.5 ±2.1	23.0 ±1.4	26.0 ±2.58	1731.8 ±28.1
Black-locust	46.5 ±7.4	59.2 ±7.4	29.6 ±1.2	23.7 ±2.7	14.7 ±3.3	54.3 ±2.6	28.3 ±1.1	28.9 ±2.6	890.0 ±218.1
Hum-mock	129.6 ±24.3	137.2 ±18.3	37.5 ±2.0	20.7 ±3.1	4.2 ±1.2	63.3 ±4.9	29.2 ±1.2	29.2 ±2.8	1195.6 ±209.5

ed significantly more eggs than plots with smaller host plants. Host plant number significantly partitioned plots with smaller (< 45 cm) host plants into two groups; plots with more than 135 host plants hosted more eggs than plots with fewer host plants (Fig. 3).

After the flight period 471 larvae were counted in the plots. Larvae were present in 48 of the 115 plots. Larvae number was significantly higher in plots of hummock vegetation type than in black-locust, open and poplar type. The second node of the conditional inference tree was only marginally non-significant and partitioned black-locust and open plots from poplar plots (Fig. 3). The regression tree with the undergrowth parameters showed that food plant height partitioned the sample into three category, plots with the highest number of larvae were plots with higher than 75 cm food plants, fewer larvae were in plots with food plants between 75 and 60 cm, and the lowest number of larvae were in plots with shorter than 60 cm food plants (Fig. 3).

The four vegetation types differed in number of food plants, height of food plants, cover of bare ground and light intensity (Table 2). Relying on

Table 3. Results of conditional inference trees on the habitat characteristics as dependent and vegetation type as independent variables. Significant values are bold.

habitat parameter	group1	group2	p
bare ground	black-locust, hummock, open	poplar	**<0.001**
food plant height1	black-locust, hummock, open	poplar	**0.013**
food plant height2	hummock	black-locust, open, poplar	0.117
food plant number2	hummock	black-locust, open, poplar	**0.001**
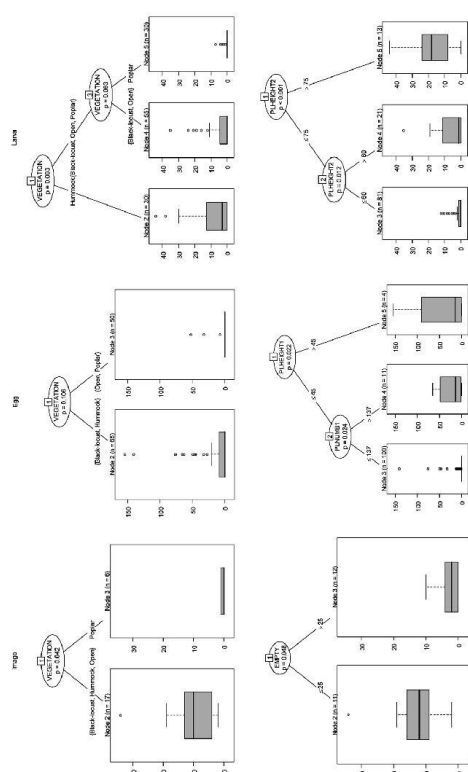
Fig. 3. Conditional inference trees show the effect of vegetation type and undergrowths parameters on the abundance of the three life stages. Nodes show the separating value of the effective parameters with their significance level, while branches show the mean and size of grouped samples. 'EMPTY': percentage of bare ground; 'PLHEIGHT1': food plant height at the first survey; 'PL-HEIGHT2': food plant height at the second survey; 'PLNUMB1': food plant number at the first survey.

Table 4. Comparing undergrowth parameters of vegetation types. Results of Multiple Comparison after Kruskal-Wallis test.

	Food plant height 1			Food plant number 1			Food plant number 2		
	observed difference	critical difference	difference	observed difference	critical difference	difference	observed difference	critical difference	difference
Black-locust–Hummock	7.9	9.5	False	9.7	10.0	False	9.3	10.0	False
Black-locust–Open	5.2	10.7	False	1.5	11.2	False	11.4	11.2	True
Black-locust–Poplar	0.4	10.0	False	4.1	10.0	False	1.8	10.0	False
Hummock–Open	13.2	11.1	True	8.3	11.6	False	2.2	11.6	False
Hummock–Poplar	8.3	10.4	False	13.8	10.3	True	11.1	10.3	True
Open–Poplar	4.9	11.5	False	5.6	11.6	False	13.3	11.6	True

	Bare ground 1			Bare ground 2			Height of undergrowth		
	observed difference	critical difference	difference	observed difference	critical difference	difference	observed difference	critical difference	difference
Black-locust–Hummock	6.5	20.9	False	22.5	21.9	True	1.4	20.9	False
Black-locust–Open	9.3	23.6	False	17.8	24.7	False	28.7	23.6	True
Black-locust–Poplar	49.3	22.0	True	31.2	21.9	True	2.7	24.3	False
Hummock–Open	2.8	24.3	False	4.8	25.4	False	27.4	24.3	True
Hummock–Poplar	55.9	22.8	True	53.8	22.7	True	4.0	22.8	False
Open–Poplar	58.7	25.2	True	49.0	25.4	True	31.4	25.2	True

Kruskal-Wallis tests some vegetation type characters differed in the four veg-
etation type. Food plant height was different in the four vegetation category at
the first survey (df = 3, χ^2 = 11.0, p = 0.011), it was higher in hummocks than in
open transects based on Multiple Comparison test after Kruskal Wallis (Table
4) (observed difference = 13.2, critical difference = 11.1, p = 0.05). The differ-
ence became non-significant for the second survey (df =3, χ^2 = 3.7, p = 0.291).
Food plant number at the first survey was significantly higher in hummock
vegetation type than in others (df = 3, χ^2 = 13.2, p = 0.004), while at the second
survey it was significantly higher in hummock and open patches than in black
locust and poplar patches (df = 3, χ^2 = 15.3, p = 0.002) (Table 4). Similarly, light
intensity was also significantly higher at hummocks and open patches than
in black locust and poplar ones (df = 3, light intensity χ^2 = 12.7, p = 0.005).
Bare ground cover was significantly higher in poplar patches than in all other
vegetation types (first survey: df = 3, χ^2 = 12.1, p = 0.007, second survey: df =3,
χ^2 = 47.6, p < 0.01) (Table 4). Height of undergrowth at the first survey was
significantly higher in black-locust, and hummock, than in open and poplar
quadrates (df =3, χ^2 = 14.5, p = 0.002) (Table 4). During the second survey, there
was no significant difference in height of undergrowth (df = 3, χ^2 = 3.6, p =
0.307). There was a negative correlation between light intensity and percent-
age of bare ground cover per transects (S = 3131.36, p = 0.01, rho=-0.55), while
we found a positive correlation between light intensity and number of host
plants in the first (S = 1136, p = 0.04 rho = 0.44), and second survey (S = 631.66,
p < 0.01, rho = 0.69). There was no significant correlation between light inten-
sity and height of host plants nor in the first (S = 2030.02, p = 0.99 rho = –0.003),
neither in the second survey (S = 1274.15, p = 0.08 rho = 0.37).

DISCUSSION

Our study demonstrated that distribution of different life stages of the
southern festoon butterfly was highly uneven among food plant patches in
different vegetation types. Although distribution of adults and juvenile forms
showed quite similar patterns, we could also reveal some differences that can
be explained by different environmental conditions in distinct vegetation types.

Adult butterflies clearly avoided poplar patches, but their abundance in
the other three vegetation types was fairly similar, in other words, they used
them equally. This pattern largely coincided with the cover of bare ground
and none of the other environmental variables had significant effect on it.
However, we suppose that light intensity may play a crucial role in affect-
ing butterfly movement and distribution. Our observations on Z. polyxena
individuals suggest that the activity of this species is highly dependent on
direct sunlight (KŐRÖSI et al. unpubl. data), and we suggest that poplar stands

were avoided by the butterflies because light intensity was probably below a certain threshold. Moreover, light intensity was negatively correlated with bare ground cover. Possibly, bare ground cover described better the amount of sunlight on an area during the whole development period of the southern festoon, than once measured light intensity. Measurement of light intensity was far less precise and detailed than that of other environmental variables, and presumably this also may have caused that it did not prove to have a significant effect. Our result that bare ground and shaded microhabitat type had a negative effect on adult abundance confirms the conclusion of ČELIK (2012) that the area of host plant stands in sunny locations is strongly related with male and weakly with female adult numbers. They showed the importance of sunny food plant patches and the significance of resource overlapping. Size or amount of food plants had no effect on imago abundance, similarly to our study (ČELIK 2012). Flight activity of adult butterflies in search for nectar sources and resting places could mask the female's search for suitable oviposition sites, therefore the adults may spend time in areas with few or low quality larval food plant. However, the lack of a significant food plant effect on adults could be the result of the fact that we did not differentiate genders during our survey. Different habitat use of males and females is possible, particularly in light of male dominance in sex ratios, which was observed during in earlier MRR studies in 2003–2004 in Hungary (ÖRVÖSSY *et al.* unpubl. data) and in Slovenia (ČELIK 2012). Male dominance can lead to male harassment on females, causing different behaviour and habitat use of the two sexes. Females fly longer distances, while males have a smaller home range (ČELIK 2012). Another explanation for the lack of larval food plant effect on adults might be that food plants, which occurred in high abundance, were not a limiting factor in the study area and the study did not include areas without food plants. There are studies where the availability of larval resources did not affect the abundance of females, e.g. *Parnassius apollo* (FRED *et al.* 2006), while other large-scale studies suggest that population size of monophagous butterflies linearly increases with the density of larval food plants (KRAUSS *et al.* 2004, BATÁRY *et al.* 2007) or that adult abundance is positively correlated with the larval food plant, as in the case of *Euphydryas aurinia* (MUNGUIRA 1997).

Distribution of eggs showed a bit different pattern from butterflies as their presence and number was lower in open and poplar patches than in hummocks and black locust patches. This means that butterflies used the food plant patches in open areas, but did not lay many eggs there. Eggs were more abundant in plots where food plants were bigger and food plant number was higher. Food plant number was significantly higher in hummock (first survey), and in hummock and open patches (second survey). Food plants were significantly taller in hummock than in other vegetation types at the first sur-

vey. At the second survey the pattern was similar, but the difference was not significant. Seemingly, the number and size of food plants together can jointly explain the egg distribution. Egg distribution could differ from adult distribution in other butterfly species as well, such as *Hypochrysops halietus*, where adult density was high in a track without vegetation, but larvae were present only on the food plant (DOVER & ROWLINGSON 2005). Other studies showed that adults preferred the same habitat suitable for egg-laying, so egg density was greater where adults were more abundant, as in the case of *Aricia artaxerxes* (ELLIS 2003). Our observations on *Z. polyxena* individuals suggest that the activity of this species is highly dependent on direct sunlight (KŐRÖSI *et al.* unpubl. data). However, clearings could be too dry for eggs, and drought can be a critical factor in the larval development (SCHWEIGER *et al.* 2006). Clearings were not only dry, but were more exposed to occasional night frosts during the egg and early larval stages.

Hummocks and black-locust patches were the best oviposition sites, an observation that was confirmed by a latter study (BATÁRY *et al.* 2008), probably due to the large number and size of food plants, which had a positive relationship with the amount of larvae. Hummocks are nitrogen-rich and sunny enough to be the most suitable habitat for the food plant. To lay eggs in an area with sufficient food plant is necessary, since excessive egg load can lead to defoliation of the food plants, as in the case of *Zerynthia cretica*, which forces larval searching for food plant with increased mortality (DENNIS 1996). Although egg density depended on food plant density at this scale, in a latter study on egg distribution we showed that at the level of individual food plant shoots the surrounding food plant density had no significant effect on egg density (BATÁRY *et al.* 2008).

Larvae showed a different distribution from eggs and butterflies, since they were significantly most abundant in hummock patches. Larvae number was also lower in poplar patches than other vegetation types, but this difference was marginally non-significant. We recorded larvae in much more plots than eggs, probably because eggs are usually laid in small clusters by females and caterpillars may disperse to reduce competition. Larvae number was significantly affected by food plant height, indicating that food plant biomass may be an important factor in larval survival and development. Food plant height was highest in hummocks and lowest in poplar patches, just like the number of larvae. The fact that larval distribution differed from egg distribution suggests that larval survival was highest in hummock patches. Number of larvae was highest in hummocks, medium amount was observed in black-locust and open patches and only occasionally was observed in poplar plantation. The difference in significance of egg and larval distribution might mean that the initial distribution of the recruits changed during larval development.

This phenomenon could be explained by the fact that females do not necessarily can select the best host and larvae may reject the given plant individual they hatched on (BERNAYS & CHAPMAN 1994). It is also possible that larvae were moved from less suitable microhabitats and/or had a higher mortality rate on them. Egg-laying is time consuming, besides choosing the best oviposition places, females should also optimise the number of eggs laid. This can lead to aggregated egg distribution, as larvae were less aggregated, larval movement is likely. Larval movement could reduce competition among conspecifics, compensate weak maternal choice or changes in habitat quality after egg-laying. Adults strongly preferred hummocks and black-locust patches. Egg distribution showed similar pattern, although it was not so pronounced. This pattern changed when larvae hatched. Hummocks hosted most of them; black-locust and open patches had fewer larvas while poplar plots were almost free of larvae. This pattern change could be the result of different egg and larval survival in the four vegetation types. As black-locust was coming to leaves, transects in black-locust patches became more shaded therefore, it may be turn to an ecological trap, since after the egg-laying period it became less suitable for larval development than in hummocks.

Changes in habitat quality during larval development were the result of both the growing shading of black-locust trees, and the proliferation of undergrowth, which could delay or inhibit the development of food plant and/or larvae. Lower temperatures might force the larvae to leave the hatching place because of either increasing mortality or decreasing growth rate. MEYER and SISK (2001) found that canopy cover is an important factor in mortality of eggs and larvae, since too much light can dry out eggs, while overshading may reduce food plant vigour. Our results showed that the height of food plants positively affected both presence and density of larvae. This emphasizes the importance of a sufficient amount of food plant to avoid defoliation and larval starvation (DENNIS 1996).

The traditional food plant based definition of habitat patch would fail in the case of the southern festoon in the study area. Though food plants itself were available in the study site in large quantity, however, the suitability of food plant patches was different in the four habitat types. The poplar plantation seems to be the poorest habitat for this species; each of the three studied life stages was less numerous there. At first sight suitable food plant patches of the poplar habitat were not used by the butterflies and therefore can be regarded as low quality habitats or even an ecological trap (ROBERTSON *et al.* 2013), as its quality is decreasing during the butterfly's life-cycle. Defining the habitat based on all the necessary resources (DENNIS *et al.* 2006, VANREUSEL *et al.* 2007) would lead to more precise habitat maps, in contrast to those based merely on food plant distribution.

This study showed the importance of within-patch habitat quality, as the different life stages of this butterfly were revealed to have different habitat requirements, a result that is in concordance with other studies (Thomas 1991, Ellis 2003, Dover & Rowlingson 2005). We did not investigate the effects of size or isolation of habitat patches in this study area, which is relatively large and easily penetrable for the southern festoon. In our study we could point out the importance of habitat quality on the fine scale distribution of *Z. polyxena* and proving that within-site variation in habitat quality is very relevant to site occupancy of this species, as in the case of *Melitaea cinxia* (Thomas *et al.* 2001), *Polyommatus bellargus* (Thomas *et al.* 2001), *Thymelicus acteon* (Thomas 1983, Thomas *et al.* 2001) and *Speyeria nokomis* (Fleishman 2002).

Since the importance of human-dominated habitats is increasing due to the decline of natural habitats and decrease of natural disturbance (Robertson *et al.* 1995), the state of these plantation complexes can strongly affect the survival and reproduction of southern festoon and can offer alternative habitats for them, similarly to other insect species living in riparian forests (Allegro & Sciaky 2003). Human created habitats, like plantations can also act as ecological trap for butterflies (Robertson *et al.* 2013), therefore study on real habitat requirements of all the life stages is necessary to facilitate long-term survival of protected butterfly species.

*

REFERENCES

Allegro, G. & Sciaky, R. (2003) Assessing the potential role of ground beetles (Coleoptera, Carabidae) as bioindicators in poplar stands with a newly proposed ecological index (FAI). *Forest Ecology and Management* **175**: 275–284.

Bálint, Z., Gubányi, A. & Pitter, G. (2006) *Magyarország védett pillangóalakú lepkéinek katalógusa a Magyar Természettudományi Múzeum gyűjteménye alapján* [A catalogue of protected papilioformid butterflies of Hungary based on the collection of the Hungarian Natural History Museum]. Magyar Természettudományi Múzeum, Budapest, 136 pp.

Batáry, P., Örvössy, N., Kőrösi, Á., Vályi-Nagy, M. & Peregovits, L. (2007) Microhabitat preferences of Maculinea teleius (Lepidoptera: Lycaenidae) in a mosaic landscape. *European Journal of Entomology* **104**: 731–736.

Batáry, P., Örvössy, N., Kőrösi, Á. & Peregovits, L. (2008) Egg distribution of the southern festoon (Zerynthia polyxena). *Acta Zoologica Academiae Scientiarum Hungaricae* **54**(4): 401–410.

BERGMAN, K-O. (1999) Habitat utilization by Lopinga achine (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. *Biological Conservation* **88**: 69–74.

BERNAYS, E. A. & CHAPMAN, R. F. (1994) *Host-plant selection by phytophagous insects.* Chapman & Hall, London, 312 pp.

BULL, C. M., ZALUCKI, M. P., SUZUKI, Y., MACKAY, D. A. & KITCHING, R. L. (1985) An experimental investigation of patch use by female monarch butterflies, Danaus plexippus (L.). *Australian Journal of Ecology* **10**: 391–398.

BOURN, N. A. D. & THOMAS, J. A. (1993) The ecology and conservation of the brown argus butterfly Aricia agestis in Britain. *Biological Conservation* **63**: 67–74.

ČELIK, T. (2012) Adult demography, spatial distribution and movements of Zerynthia polyxena (Lepidoptera: Papilionidae) in a dense network of permanent habitats. *European Journal of Entomology.* 109: 217–227.

DENNIS, R. L. H. (1996) Oviposition in Zerynthia cretica (Rebel, 1904): loading on leaves, shoots and plant patches (Lepidoptera, Papilionidae). *Nota Lepidopterologica* **18**: 3–15.

DENNIS, R. L. H., SHREEVE, T. & VAN DYCK, H. (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation* **15**: 1943–1966.

DOVER, J. W. & ROWLINGSON, B. (2005) The western jewel butterfly (Hypochrysoops halietus): factors affecting adult butterfly distribution within native Banksia bushland in an urban setting. *Biological Conservation* **122**: 599–609.

ELLIS, S. (2003) Habitat quality and management for the northern brown argus butterfly Aricia artaxerxes (Lepidoptera: Lycaenidae) in North East England. *Biological Conservation* **113**: 285–294.

FISCHER, K. (1998) Population structure, mobility and habitat selection of the butterfly Lycaena hippothoe (Lycaenidae: Lycaenini) in eastern Germany. *Nota Lepidopterologica* **21**: 14–30.

FISCHER, K., BEINLICH, B. & PLACHTER, H. (1998) Population structure, mobility and habitat preferences of the violet copper Lycaena helle (Lepidoptera: Lycaenidae) in western Germany: implications for conservation. *Journal of Insect Conservation* **3**: 43–52.

FLEISHMAN, E., RAY, C., SJÖGREN-GULVE, P., BOGGS, C. L. & MURPHY, D. (2002) Assessing the roles of patch quality, area and isolation in predicting metapopulation dynamics. *Conservation Biology* **16**: 706–716.

FRED, S. M., O'HARA, R. B. & BROMMER, J. E. (2006) Consequences of the spatial configuration of resources for the distribution and dynamics of the endangered Parnassius apollo butterfly. *Biological Conservation* **130**: 183–192.

GRUNDEL, R., PAVLOVIC, N. B. & SULZMAN C. L. (1998) Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. *Biological Conservation* **85**: 47–53.

GIRAUDOUX, P. (2014) Package 'pgirmess', url: http:// perso.orange.fr/giraudoux

HANSKI, I., MOILANEN, A., PAKKALA, T. & KUUSSAARI, M. (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* **10**: 578–590.

HOTHORN, T., HORNIK, K. & ZEILEIS, A. (2006) Unbiased Recursive Partitioning: A Conditional Inference Framework. *Journal of Computational and Graphical Statistics* 15: 651-674.

KRAUSS, J., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2004) Landscape occupancy and local population size depends on food-plant distribution in the butterfly Cupido minimus. *Biological Conservation* **120**: 355–361.

KONVIČKA, M., HULA, V. & FRIC, Z. (2003) Habitat of pre-hibernating larvae of endangered butterfly Euphydryas aurinia (Lepidoptera: Nymphalidae): What can be learned from habitat composition and architecture. *European Journal of Entomology* **100**: 313–322.

LOW, M., JOY, M. K. & MAKAN, T. (2006) Using regression trees to predict patterns of male provisioning in the stitchbird (hihi). *Animal Behaviour* **71**: 1057–1068.

MEYER, C. L. & SISK, T. D. (2001) Butterfly response to microclimatic conditions following ponderosa pine restoration. *Restoration Ecology* **9**: 453–461.

MUNGUIRA, M. L., MARTIN, J., GARCIA-BARROS, E. & VIEJO, J. L. (1997) Use of space and resources in a Mediterranean population of the butterfly Euphydryas aurinia. *Acta Oecologica* **18**: 597–612.

NAGY, K., REICZIGEL, J., HARNOS, A., SCHROTT, A. & KABAI, P. (2010) Tree-based methods as an alternative to logistic regression in revealing risk factors of crib-biting in horses. *Journal of Equine Veterinary Science* **30**: 21–26.

NOWICKI, P., PEPKOWSKA, A., KUDLEK, J., SKÓRKA, P., WITEK, M., SETTELE, J. & WOYCIECHOWSKI, M. (2007) From metapopulation theory to conservation recommendations: Lessons from spatial occurrence and abundance patterns of Maculinea butterflies. *Biological Conservation* **140**: 119–129.

RAVENSCROFT, N. O. M. (1992) Habitat selection by larvae of the chequered skipper butterfly, Carterocephalus palaemon (Pallas) (Lepidoptera: Hesperidae) in northern Europe. *Entomologist's Gazette* **43**: 237–242.

R DEVELOPMENT CORE TEAM (2006) *A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

ROBERTSON, P. P. A., CLARKE, S. A. & WARREN, M. S. (1995) Woodland management and butterfly diversity. Pp. 111–122. *In:* PULLIN, A. S. (ed.): *Ecology and conservation of butterflies.* Chapman and Hall, London.

ROBERTSON, B. A., REHAGE, J. S. & SIH, A. (2013) Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution* **28**: 552–560.

SCHWEIGER, O., DORMANN, C. F., BAILEY, D. & FRENZEL, M. (2006) Occurrence pattern of Pararge aegeria (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure. *Landscape Ecology* **21**: 989–1001.

SEI, M. & PORTER, A. H. (2003) Microhabitat-specific early-larval survival of the maritime ringlet (Coenonympha tullia nipisiquit). *Animal Conservation* **6**: 55–61.

SMALLIDGE, P. J. & DONALD, J. L. (1997) Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. *Landscape and Urban Planning* **38**: 259–280.

THOMAS, J. A. (1983) The ecology and status of Thymelicus acteon (Lepidoptera: Hesperiidae) in Britain. *Ecological Entomology* **8**: 427–435.

THOMAS, J. A., THOMAS, C. D., SIMCOX, D. J. & CLARKE, R. T. (1986) Ecology and declining status of the silver-spotted skipper butterfly (Hesperia comma) in Britain. *Journal of Applied Ecology* **23**: 365–380.

THOMAS, J. A. (1991) Rare species conservation: case studies of European butterflies. Pp. 149–197. *In:* SPELLERBERG, I. F., GOLDSMITH, F. B. & MORRIS, M. G. (eds): *The scientific management of temperate communities for conservation.* Blackwell Scientific Publications, Oxford.

THOMAS, J. A., BOURN, N. A. D., CLARKE, R. T., STEWART, K. E., SIMCOX, D. J., PEARMAN, G. S., CURTIS, R. & GOODGER, B. (2001) The quality and isolation of habitat patches both

determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B* **268**: 1791–1796.

Thomas, C. D. & Hanski, I. (1997) Butterfly metapopulations. Pp. 359–386. *In:* Hanski, I. & Gilpin, M. E. (eds): *Metapopulation biology, ecology, genetics and evolution.* Academic Press, San Diego.

Thomas, C. D., Thomas, J. A. & Warren, M. S. (1992) Distribution of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**: 563–567.

Vanreusel, W. & Van Dyck, H. (2007) When functional habitat does not match vegetation types: A resource-based approach to map butterfly habitat. *Biological Conservation* **135**: 202–211.

Wahlberg, N., Klemetti, T. & Hanski, I. (2002) Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography* **25**: 224–232.

Warren, M. S. (1985) The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white Leptidea sinapsis. *Biological Conservation* **33**: 147–164.

Warren, M. S. (1987) The ecology and conservation of the Heath Fritillary butterfly, Mellicta athalia: III. Population dynamics and the effect of habitat management. *Journal of Applied Ecology* **24**: 499–513.