



**POPULATION SPATIAL STRUCTURE AND HABITAT USE OF
LARGE BLUE BUTTERFLIES (LEPIDOPTERA: LYCAENIDAE)**

**HANGYABOGLÁRKA LEPKÉK (LEPIDOPTERA: LYCAENIDAE)
TÉRBELI POPULÁCIÓSZERKEZETE ÉS ÉLŐHELYHASZNÁLATA**

Doktori (PhD) értekezés

KÖRÖSI ÁDÁM

Témavezető

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Juhász-Nagy Pál Doktori Iskola
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INTRODUCTION

The present dissertation comprises a collection of selected papers and manuscripts which have been prepared jointly with my co-authors on the population ecology of large blue butterflies (*Maculinea spp.*) and involves a preceding overview of the research topic. In this overview, instead of repeating the methods and results of the selected papers in details, I intend to clarify our aims by giving an overview of the biology of *Maculinea* butterflies, provide a brief review of the methods applied, results obtained, enlighten their significance in population ecology and discuss the implications for conservation of large blue butterflies.

The worldwide loss of biodiversity is likely to be the greatest crisis that humanity has ever faced. Butterflies are part of the natural systems that support our life and are increasingly destroyed by human activities. However, they also may help us to ameliorate this critical situation as they have become essential model and testing systems in many fields of biology, such as ecology, evolutionary biology, systematics, animal behaviour and conservation biology (e.g. Boggs et al. 2003). If we want to preserve a habitable planet we have to know how it works and butterflies can provide a good model system on which much research effort can be concentrated to acquire the needed information. The main reason they can play this important role is that they have attracted much attention of naturalists and dedicated amateurs for a long time producing many books and papers on their taxonomy, distribution and life history. This knowledge provides the foundation needed before a group can serve such crucial functions (Ehrlich 2003). The present work aims to contribute to the understanding of the ecology of butterflies by providing information about their population structure, habitat use and conservation biology.

Spatial structure of butterfly populations

Nowadays, space is introduced in various ways into all fields of ecology and population biology generally, and spatial structure is widely seen as a vital ingredient of better and more powerful theories (Hanski & Simberloff 1997; Tilman & Kareiva 1997). Metapopulation approach has emerged in the field of spatial ecology and become a subtle and finely elaborated theory that has by now been firmly established in population biology and beyond. The two key premises in the metapopulation approach are that populations are spatially structured into assemblages of local breeding populations and that dispersal among the local populations has some effect on local dynamics, including the possibility of recolonization of empty habitats after extinction (Hanski & Simberloff 1997).

Butterflies have played a disproportionate role in the study of metapopulations due to several reasons (Thomas & Hanski 1997). First, butterfly populations are often structured in space in a manner that is broadly consistent with the metapopulation concept. Second, the ecology of butterflies is well known, especially in Europe. Third, exceptionally large proportion of butterflies has already declined, become endangered or gone extinct (*e.g.* Warren 1993; Maes & Van Dyck 2001; Wenzel et al. 2006). Extensive studies of the spatio-temporal dynamics and structure of butterfly populations identified many categories of population type, but empirical population systems are difficult to assign to single categories (Thomas & Kunin 1999). The classical metapopulation approach can be applied to many populations of butterflies (*e.g.* Harrison et al. 1998; Hanski et al. 1994; Schtickzelle et al. 2002; Wahlberg et al. 2002) and may provide a conservation framework for species confronted with habitat loss and fragmentation (*e.g.* Wahlberg et al. 1996; Mousson et al. 1999; Schtickzelle & Baguette 2003a). However, several spatially structured butterfly populations do not correspond to the classical metapopulation theory, due to the low rate of colonization and extinction of local populations or the high patch occupancy, while the dynamics of the metapopulation may be far from equilibrium (for a review see Baguette 2004). Moreover, several authors have stressed that gathering information on the local population dynamics and within-habitat movement are very important to ensure the validity of population viability analyses (Baguette & Schtickzelle 2003; Lindenmayer et al. 2003). Finally, the movement processes between habitat patches (and subpopulations) have been thoroughly studied empirically (*e.g.* Baguette et al. 2000; Petit et al. 2001; Kuras et al. 2003) and a number of approaches have been developed to extract movement parameters from data collected in heterogeneous landscapes (*e.g.* Hanski et al. 2000; Wilson & Thomas 2002; Morales et al. 2004). Some of them can even estimate the parameters of movement behaviour itself (Ovaskainen 2004), but assume that individuals perform a correlated random walk, eventually with different rules in different habitats. Recently a few authors demonstrated that movement pattern within habitat patches may depart from the random walk (Körösi et al. 2008; Hovestadt & Nowicki 2008). Despite of this controversial relationship between observed movement patterns and model assumptions, and knowledge gaps in local population processes this field of research has attracted little attention.

Biology of large blue butterflies

Research on the biology of *Maculinea* species began in the late 70's when strong decline of the large blue butterfly (*M. arion*) in Britain, which had been observed for decades,

forecasted its extinction (Thomas 1980). The first investigations concentrated on the butterflies' special life cycle and their interactions with the food plant and host ant species. These studies revealed, that uniquely among European butterflies, *Maculinea* species are obligate social parasites of *Myrmica* ant colonies (e.g. Elmes & Thomas 1987), which makes them an exceptional good model system for evolutionary and community ecological studies.

Females of *Maculinea* butterflies lay their eggs on specific food plants where caterpillars hatch after two weeks and feed on the seeds until they reach their fourth instar. Thereafter, they descend to the ground and await being discovered and adopted by foraging workers of specific *Myrmica* species. Ant workers carry them into their nests, where *Maculinea* caterpillars either predate on ant larvae (*M. arion*, *M. teleius* and *M. nausithous*; see Chapman 1916; Frohawk 1916; Thomas 1992) or mimic ant grubs and are fed by workers through trophallaxis ('cuckoo-feeders', *M. alcon*; Elmes et al. 1991a), which is considered as a more productive (Thomas & Elmes 1998) and evolutionarily advanced form of myrmecophily (Thomas et al. 1991; Fiedler 1998; Als et al. 2004).

The two feeding strategies have different consequences for the ecology of butterflies. Predatory *Maculinea* caterpillars suffer from intraspecific scramble competition in the ant nests, because consuming all ant larvae cause the death of caterpillars from starvation. Thus their survival rate dramatically decreases with the increasing number of caterpillars per nest (Thomas & Wardlaw 1992). On the other hand, there is a contest competition among cuckoo-feeder caterpillars, which means that at least a few of them can certainly complete their development even at very high density (Thomas & Elmes 1993). Moreover, as cuckoo-feeder caterpillars are directly fed by the workers, one trophic level (that of the ant larvae) is absent from their food chain compared to the predatory species, which results in a higher carrying capacity of the host ant colonies of cuckoo-feeder butterflies. For example, 1 or at most 2 caterpillars can be reared by a nest of *Myrmica sabuleti*, host of the predatory *M. arion*, while on average 5–6 adult butterflies can emerge from a host ant nest in *M. alcon* (and '*M. rebeli*') (Thomas & Elmes 1998). Therefore, predatory species must spread their eggs among more host ant nests than cuckoo-feeders to reduce the competition between offsprings. As a consequence, the coincidence of food plant and host ants must be as high as >50% for predatory species (Thomas & Elmes 1998; Thomas et al. 1998a), whereas this overlap is thought to be usually between 15 and 30% for cuckoo-feeders (Elmes et al. 1996).

Depending on the feeding strategy of *Maculinea* caterpillars, their ichneumonid parasitoids use different ways to find them. Cuckoo-feeding caterpillars (*M. alcon*) are attacked by *Ichneumon eumerus*, which enters into the *Myrmica* nests infected by *Maculinea*

and lays eggs in all caterpillars (Thomas & Elmes 1993). The parasitoid wasp *Neotypus melanocephalus* attacks *Maculinea nausithous* and *M. teleius* by searching for caterpillars on the flowerheads of the butterflies' food plant *Sanguisorba officinalis* (Tartally 2005; Anton et al. 2007).

Additionally to their specific life-cycle, *Maculinea* butterflies provide exceptions to normal insect growth rules (Elmes et al. 2001). In the phase of rapid development on the food plant, caterpillars reach their final instar within two or three weeks, but gain only 1% of their final body mass (Elmes et al. 1991b; Thomas & Wardlaw 1992). During the final carnivorous instar their growth rate is >10 times higher than predicted by extrapolating the early growth rate, which is very similar to the growth pattern of *Myrmica* ants. This growth pattern of caterpillars is another adaptation that enables them to penetrate and exploit host ant colonies, since last instar caterpillars must be small enough to be integrated as brood mimics into ant social systems and they must survive long periods of starvation and grow rapidly when food is abundant (Elmes et al. 2001). Moreover, ~25% of caterpillars take 10 months to complete their final instar, while the remaining proportion requires 22 months to mature and these two forms are morphologically identical at the prepupation stage (Thomas et al. 1998a; Witek et al. 2006). This polymorphic growth rate is otherwise very rare in the animal kingdom, but seems to be common in social parasites of ants and appears to be genetically controlled (Schönrogge et al. 2000). This polymorphism is a further adaptation to efficiently exploit the limited, yet steady, daily supply of food available for social parasites of host ant colonies. It also reduces the kin competition between offsprings, because biennial caterpillars gain most of their body mass when one-year developers are already out of the ant nests (Hovestadt et al. 2007).

The ability of *Maculinea* butterflies to penetrate host ant nests is ensured by their chemical mimicry and camouflage among others. The caterpillars produce surface chemicals, mimetic compounds and other secretions that closely mimic the profile of their main host and allow that *Myrmica* ants recognize them as conspecific broods (Akino et al. 1999). These findings explained well the high host-specificity of *Maculinea* butterflies which was found in the earlier studies (Thomas et al. 1989). However, large-scale investigations of host-specificity revealed that host-specificity of some *Maculinea* species can show high geographical variation (Elmes et al. 1994) and even local adaptations, while others utilise mainly a single host species (for more details see Pech et al. 2007; Sielezniew & Stankiewicz 2008; Tartally & Varga 2008; Tartally et al. 2008; Witek et al. 2008).

Early studies on population biology of *Maculinea* butterflies attempted to quantify the functional relationships of butterflies with food plants and host ants, and tried to model the consequences of these interactions on population dynamics. By estimating the mortality of all life stages these models clearly indicated that the survival of the butterfly in the ant nest was disproportionately more important to its population than was competition on the food plant (Hochberg et al. 1992). Changes in the population of the plant had virtually no impact on the butterfly population. Spatially explicit models predicted that the largest populations of butterflies should occur in habitats with intermediate host plant density (Hochberg et al. 1994). As food plants transmit *Maculinea* caterpillars to the ant nests, very high food plant density could cause the overexploitation of host ants and thus the decline (or extinction) of butterflies. The predictions of this apparent competition hypothesis were empirically tested later (Thomas et al. 1997). Moreover, *Maculinea* populations were found to be very stable with exceptionally small annual fluctuations in their size (Elmes et al. 1996). In further models spatial ruggedness of habitat quality within sites was found to have a substantial effect on the butterfly, which often failed to persist on very rugged sites (Clarke et al. 1997). Despite being free-ranging over the whole site, the butterfly's dynamics may depend on the arrangement of habitat quality at a finer spatial scale, due to its interactions with ant species possessing narrower habitat niches and more localized dispersal (Clarke et al. 1998).

All these thorough examinations focussed on the xerophilous ecotype of *M. alcon* ('*M. rebeli*'), a cuckoo-feeding species. However, very few attempts have been made to empirically study the population structure and dynamics of predacious *Maculinea* butterflies until the recent past (for some exceptions see Thomas 1984b, 1995; Thomas et al. 1998b). Studying sympatric populations of *M. nausithous* and *M. teleius* in Poland Nowicki et al. (2005) found a female-biased sex ratio and little year-to-year variation in population sizes for both species. In addition, inter-patch mobility of butterflies was low in spite of relatively short distances between patches. In a metapopulation-scale study an almost complete occupancy of food plant patches was found for all three *Maculinea* species inhabiting marshland meadows (Nowicki et al. 2007). Food plant availability was the main factor limiting population densities for *M. alcon*, but not for the predacious *M. nausithous* and *M. teleius*, for which patch size and shape mattered the most. Small and highly internally fragmented patches supported higher densities of these two species. The negative density–area relationship seems to be typical for butterfly populations (Hambäck & Englund 2005), while internal fragmentation of patches can increase the proportion of host plant free edges, which may serve as refugia for the host ants (Nowicki et al. 2007). These studies proved that

local population densities and dynamics can be important for metapopulation functioning and long-term persistence of *Maculinea* butterflies. More recently Anton et al. (2008) revealed that the density of *M. nausithous* was limited by the density of its host ant (*Myrmica rubra*) and host plant density had no effect on the density of any stage (egg, larval, adult) of the butterfly.

The role of *Maculinea* butterflies in nature conservation

The conservation of butterflies has been of a great concern for many years in Western Europe, especially in Britain (see Thomas 1984a, New et al. 1995; Pullin 1995). Aesthetic values of butterflies have attracted the attention of many devoted naturalists for centuries, thus a huge amount of data have been collected on their abundance and distribution. The severe decline of several species detected in the 60's urged the conservationists to take actions for their preservation. A Butterfly Monitoring Scheme (BBMS) was developed (Pollard & Yates 1993) and monitoring activities as well as ecological researches were started (see for example Dennis 1992, Pullin 1995). Nowadays, as they are surprisingly representative of changes in abundance and distribution of many other invertebrate taxa, butterflies are widely used as an indicator group (Thomas & Clarke 2004, Thomas 2005). In addition, it has recently been shown that butterflies have experienced greater declines than plants and birds in the UK (Thomas et al. 2004). Among the different species of UK butterflies experiencing changes, Warren et al. (2001) demonstrated that specialist species had declined to a significantly greater extent than generalists during the past quarter century.

Despite many conservation attempts, *Maculinea arion* became extinct in Britain in 1979, shortly after the research had uncovered the key to its decline. The proximal cause of final extinction of the last population was an unusual coincidence of two severe summer droughts in successive breeding seasons (Thomas 1980), illustrating the inherent vulnerability of any population once it is reduced to low numbers. Based on the knowledge of its ecological requirements, *M. arion* was successfully re-established in Britain later (Thomas 1987), providing an early example for conservation practitioners for future re-establishments of threatened insects with specific life history. The complexity of their conservation lies in that *Maculinea* butterflies can persist on sites with sufficient food plants and host ant colonies. As the key factor regulating *Maculinea* populations is the variation in the survival of caterpillars in ant nests (Thomas 1977), as big proportion of caterpillars should be adopted as possible. Thus the coincidence between food plants and host ants must be high (e.g. >50% for *M. arion*; Thomas & Elmes 1998), but food plants should be dispersed, because if they are too

aggregated a few ant nests collect all the *Maculinea* larvae. Moreover, in the case of predatory species, host ant colonies must be sufficiently large to produce ant grubs that caterpillars need to eat (Thomas & Wardlaw 1992). Host ants are closely adapted to microclimatic conditions, therefore they have much narrower niches than food plants and are more sensitive to changes in vegetation structure and habitat management (Elmes & Thomas 1992; Elmes et al. 1998). Thus the conservation of *Maculinea* butterflies involves the maintenance or restoration of seral stages that have become rare in modern landscapes. This kind of ‘niche-conservation’ can have benefits for many other species depending on similar types of habitat and makes *Maculinea* butterflies useful ‘umbrella’ species.

However, due to their complex life history the dynamics of *Maculinea* populations is intrinsically cyclical or chaotic (Mouquet et al. 2005a), while tripartite interactions among the butterfly, its food plant and host ant cause that the result of different conservation strategies depends on the actual successional stage of a given site (Mouquet et al. 2005b). Moreover, latitude, altitude and climate have major influence on the effects of habitat management on *Maculinea* sites (Thomas et al. 1998c). Therefore, it is impossible to develop general strategies for the conservation of *Maculinea* butterflies in Europe, and management should be conducted on a case-by-case basis. Furthermore, large blue butterflies are exceptionally sensitive to environmental change, giving them an important role as indicators of habitat deterioration (Thomas et al. 2005). All the facts and phenomena mentioned above contributed to that *Maculinea* butterflies have become flagship species for European nature conservation (Thomas 1995; Thomas & Settele 2004). All species are listed by the Annex II or Annex IV of the Habitat Directives, since they have suffered several extinctions at local and national scales (Munguira & Martin 1999) and are among the most endangered butterflies in Europe (vanSwaay & Warren 1999) still showing declining population trends (Wynhoff 1998a).

AIMS AND QUESTIONS

Although both demographic and movement processes of local populations are suspected to have major influence on functioning and persistence of butterflies, little attention has been devoted to studies on local dynamics and patterns. Even *Maculinea* butterflies are understudied from this aspect in spite of the fact that they are recognized as low-mobility species and they have low population turnover arising from their high occupancy of food plant patches and stability of their population sizes. Moreover, they have been of a great

conservation concern for many decades, therefore a sound knowledge on the most important factors affecting their density, movement, reproduction rate and habitat use would be essential. This necessity outlined our main aims and objectives which I overview below.

Study I. Species-specific distribution of two sympatric *Maculinea* butterflies across different meadow edges

The scarce large blue (*M. teleius*) and the dusky large blue (*M. nausithous*) butterflies use the same food plant (*Sanguisorba officinalis*) and co-occur on marshland meadows in Hungary. These habitats are very often endangered by different human activities that result in their fragmentation. An important consequence of habitat fragmentation is the increase of edge habitats. Populations at the edges are exposed to changed biotic and environmental conditions partly influenced by the neighbouring habitat or association (Tschamntke et al. 2002). This phenomenon is termed edge effect which may have impact on animals on different levels (individual, population, community) (Saunders et al. 1991). We aimed to study how edges affect the distribution of sympatric populations of two *Maculinea* species within meadow fragments. We investigated the effects of distance from edge and edge type on the density of butterflies. At the same time we measured the food plant density and some microclimatic parameters to explain the observed patterns in the distribution of the two species.

Study II. Different population structure and habitat use of two sympatric *Maculinea* butterflies at small spatial scale

We were interested in whether niche segregation of the dusky large blue (*M. nausithous*) and the scarce large blue (*M. teleius*) could be detected on the scale of local populations or habitat patches embedded in a heterogeneous landscape. Therefore, we examined the microdistribution and movement pattern of sympatric populations of these butterflies within one small habitat fragment. An intensive mark–release–recapture sampling was carried out on an abandoned marshy meadow in the Órség National Park. The relationships between the distribution of butterflies and environmental variables were assessed to find species-specific patterns. As we had previously found that *M. nausithous* preferred the proximity of forests, in this study we aimed to reveal how the proportion of afforested edges influence the microdistribution of the two studied butterflies. Furthermore, we related the emigration rate

of butterflies to some environmental variables (such as area, forest proportion) and the density of butterflies, and we performed an explorative analysis of movement distances to find species-specific patterns in their habitat use.

Study III. Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies

The movement of butterflies within habitat patches is usually assumed to be random, although few studies have shown this unambiguously (Kareiva & Shigesada 1983; Root & Kareiva 1984; Schtickzelle et al. 2007). Two contradictory hypotheses exist to explain the movement and distribution of adult *Maculinea* butterflies within habitat patches: (1) due to the high spatial variance of survival rates of caterpillars, the ‘risk-spreading’ or ‘bet-hedging’ hypothesis predicts that females will tend to make linear flight paths to maximize their net displacement and scatter the eggs as widely as possible (Root & Kareiva 1984); and (2) recent mark–release–recapture analyses suggest that within-patch displacement of some *Maculinea* species is constrained and that adults may establish home ranges (Hovestadt & Nowicki 2008). Moreover, there has been a strong debate on what factors influence the food plant selection for oviposition by female *Maculinea* butterflies. In particular, the presence of host ants beneath the food plant has major effect on the survival of caterpillars, but how this factor affects the food plant selection of butterflies has been evaluated inconsistently (Van Dyck et al. 2000; Thomas & Elmes 2001; Musche et al. 2006). Here we tried to test both hypotheses on the movement behaviour of females of *Maculinea alcon* by analysing the individual movement patterns and study their oviposition preferences by direct observations of egg-laying. We also investigated whether egg-laying is time constrained, which would enhance the trade-off between flying and egg-laying. As most of our works concentrated on the population structure of *M. teleius* and *M. nausithous*, the present study would have been better to deal with some of these species in order to relate individual movement and behavioural patterns to the distribution on the population level. Unfortunately, our such efforts failed to collect sufficient datasets. Moreover, the direct observation of egg-laying is much more difficult in the case of *M. teleius* and *M. nausithous* than for *M. alcon*, since the former species hide their eggs within the inflorescences of their food plant, invisibly for human observers.

Study IV. Effects of mowing on the population of the scarce large blue, its food plant and host ants in SW Hungary

Most species occurring in European landscapes are adapted to more or less intensive human land use. In Hungary, the long-term persistence of *Maculinea* butterflies inhabiting marshy meadows can be ensured by regular grazing or mowing, otherwise the habitats become overgrown by shrubs and invasive weeds, and finally afforested. However, very few studies have investigated the effects of grassland management on the persistence and abundance of *Maculinea* butterflies and their main resources (Grill et al. 2008). The very poor scientific evidence does not provide the nature conservation with a good guidance for the management of grasslands inhabited by *Maculinea* butterflies. There are still several large (meta)populations of *M. alcon*, *M. nausithous* and *M. teleius* in the Órség National Park in W Hungary, where traditional animal husbandry and small-scale farming practice have almost disappeared in the last few decades. As a consequence, most meadows in this region are erratically mown or abandoned, which seriously endangers the populations of large blue butterflies. Abandonment may cause habitat loss, while inappropriate timing of mowing can seriously damage the populations by highly increasing larval mortality (Johst et al. 2006). In 2007, we started a long-term management experiment on marshy meadows in the Órség NP to find the most appropriate timing and frequency of mowing for the persistence (and possibly the growth) of *Maculinea* populations. We tested the effects of four different mowing regimes – which are supposed to be economically feasible – on the density of butterflies, their food plants and the frequency of their host ants. By involving more than one meadows we could account for the between-site variation as well. Our results are preliminary, as the analyses were based on a sampling in 2008 summer, which is a very short period for a management study.

MATERIALS AND METHODS

Study species

Previously five species of the genus *Maculinea* had been recorded in Europe (e.g. Thomas 1995), but recent phylogenetical studies based on either genetic (Als et al. 2004) or morphometric data (Pech et al. 2004) proved that only four species of large blue butterfly exist on the continent. Detailed analyses on populations of *Maculinea alcon* (Denis et Schiffermüller, 1775) and *Maculinea rebeli* (Hirschke 1904), which had been earlier

considered as a distinct species, showed no genetic divergence between them and therefore they should be regarded as different ecotypes of the same species (*M.alcon*) (Bereczki et al. 2005, 2006; Pecsénye et al. 2007). The most recent total evidence analysis, based on a combination of morphological and ecological characters with genetic sequences, revealed that the genera *Maculinea* and *Phengaris* are not monophyletic with regard to each other, thus *Maculinea* Van Eecke, 1915 syn. n. is considered a junior synonym of *Phengaris* Doherty, 1891 (Fric et al. 2007). However, in the ecological and conservation biological publications the generic name *Maculinea* Van Eecke, 1915 is widely accepted and used. Therefore, I follow here for simplicity this most frequently used and established generic name.

We studied three species of *Maculinea* butterfly. The xerophilous ecotype of *M.alcon* (denoted as *M.rebeli* in **Study III** and in references cited therein) occurs on dry calcareous grasslands in Hungary. It is on wings from mid-June to mid-July and uses the cross-leaved gentian *Gentiana cruciata* (L.) as the main larval food plant. Caterpillars are hosted mainly by *Myrmica sabuleti*, *M.scabrinodis* and *M.schencki*, but occasionally by other *Myrmica* species as well (Tartally et al. 2008). Females lay single eggs on leaves and buds of the gentians. Caterpillars in the ant nest are fed by workers through trophallaxis ('cuckoo-feeding') (Elmes et al. 1991a).

Maculinea nausithous (Bergsträsser, 1779) and *M.teleius* (Bergsträsser, 1779) both occupy marshy meadows, where their food plant, the great burnet (*Sanguisorba officinalis*) is abundant. However, *M.nausithous* has a restricted distribution in Hungary occurring in the Transdanubia only. Adult butterflies oviposit in the flowerheads of the food plant where caterpillars feed on the seeds for 2–3 weeks (Thomas 1984b). Some authors found that different developmental stage and size of flowerheads are preferred by ovipositing females of the two species (Figurny & Woyciechowski 1998; Thomas & Elmes 2001). After a few weeks of feeding on the seeds, caterpillars descend to the ground and await adoption by host ant workers, which carry them into their nest where caterpillars predate on the ant brood. In Hungary, *Myrmica rubra* is the only known host ant of *M.nausithous*, while the primary host ant of *M.teleius* is *Myrmica scabrinodis*, although four additional ant species are also recorded as its host (*M.gallienii*, *M.rubra*, *M.salina*, *M.specioides*) (Tartally & Varga 2008). In our study area, the flight period of the two butterflies overlaps (from early July to late August).

Study sites

Our field studies were carried out in two regions in Hungary. Study area of **study III** was located at Vértesszomszma in the Vértés Mountains in Central Hungary (Duna-Ipoly National Park, 47°26' N; 18°25' E; 365 m a.s.l.) Sampling was conducted on a section of grassland meadow (~0.8 ha) on the fringe of an oak-hornbeam forest. The meadow was surrounded by pine plantation on three sides and a native oak forest on the fourth. The site had been abandoned for a long time and become overgrown by some saplings and scrubs.

Study I, II and IV were carried out in the Őrség National Park in Western Hungary. Site of **study II** was at Kercaszomor in the Kerca stream valley (46°46' N; 16°18' E; 240 m a.s.l.). It was a piece of a marshy meadow in a mosaic landscape. Approximately half of the study site had been abandoned since 1995, while the other half had been mown erratically and seemed unsuitable for the butterflies in the sampling period and therefore was not sampled (Fig. 1). In the abandoned part of the meadow, apart from a few patches of sedges (*Carex* spp.), willow shrubs (*Salix* spp.) and invasive weeds (*Solidago* spp.), the common food plant (*Sanguisorba officinalis*) of the two study species was growing in high-density patches providing suitable habitat for both butterflies.

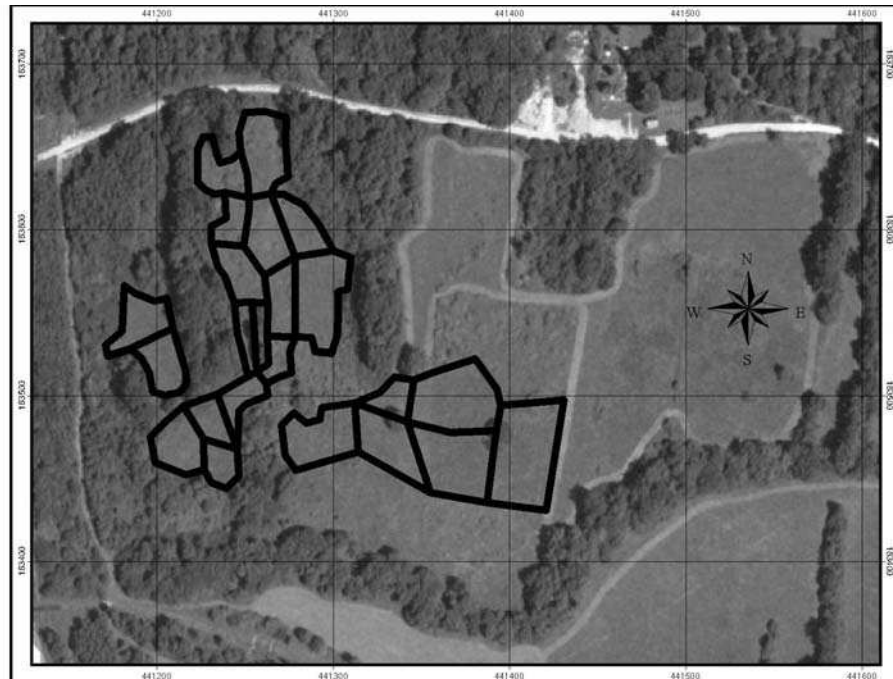


Figure 1. Aerial photo of the sampling area of **Study II** provided by the Őrség NP Directorate. Thick black lines delineate the 22 sampling units on the abandoned half of the meadow. Unsampld eastern and northern parts of the meadow were erratically mown, while the southern part was abandoned and covered by sedges. Grid cell width represents 100 m.

Study I and **IV** were conducted in the Szentgyörgyvölgyi stream valley at Velemér (46°44' N; 16°21' E; 204 m a.s.l.) and Magyarszombatfa (46°45' N; 16°19' E; 210 m a.s.l.) The area of the valley along the stream was characterized by meadows and croplands disrupted by small roads. Directly next to the stream there was a dense alder tree strip. According to the traditional farmland practice the first mowing of the year was in May and the second in late August or early September and it took place at a small spatial scale. Nowadays most meadows are mown once a year or every second or third year and there is no control on the timing of management during the season.

Sampling methods

We applied three main methods for sampling *Maculinea* populations: (i) Mark-release-recapture (MRR), (ii) transect counts and (iii) tracking of individual butterflies. MRR sampling was carried out in several studies (**II**, **III** and **IV**) to estimate survival rate, average lifespan, population size or sex ratio and to characterize population dynamics within the flight season. Moreover, by locating the position of each capture event we were able to analyze the spatial distribution and within-habitat movement pattern of butterflies (**Study II**). Butterflies were captured by net and, after the determination of sex and species, they were marked on the underside of hindwings with a unique identity code using fine-tipped waterproof pen. Specimens were released immediately thereafter. Date, time and location of captures were registered. This marking method is widely used and known to have no effect on the behaviour and survival of butterflies. Sampling was performed as weather permitted (under warm, sunny and calm conditions). We paid attention to keeping the number of field workers constant in order to standardise the sampling effort. In **Study IV**, the sampling sites on each meadow were divided into four strips of equal area according to the management regimes tested. The four regimes involved mowing in May, mowing in September, mowing in May and in September, and there was an unmown type for control. Each strip was divided into 20×20 m squares within which 10×10 m squares were laid down. Butterfly density was sampled in the 20×20 m squares, while food plant quantity and host ant frequency were sampled in the smaller quadrats. Butterflies were sampled by MRR method: 5 minutes were spent in each square by one person engaged with capturing and marking butterflies. The number of food plant flowerheads was counted, while host ants were sampled on four baits within the 10×10 m squares.

Transect counts are not appropriate to yield estimations on absolute population sizes but enable us to establish the relative abundance of animals. This method was used in **Study I**, where we designated four (two pairs) 50 m long and 5 m wide transects on each of 10 meadows. One transect pair was situated at the so-called tree edge: one transect directly next to the trees and the other one 15 m further inside parallel to the edge transect. Another transect pair was laid down in the same way at the so-called road edge next to a narrow paved or unpaved road with no trees or bushes and very low traffic. The number of butterflies was detected by walking along the transects once everyday during the peak of flight period (August 2006). Field workers walked along the transects with a standard velocity (2 min per transect) and counted the number of butterflies while taking care not to count any individual more than once. Sampling was carried out on sunny days without strong winds, from 9:00 a.m. until 4:00 p.m. At each transect count we also measured air temperature, air humidity and wind speed. Blooming shoots of the food plant were counted once on each transect in a 1 m wide strip.

If movement pattern and behaviour of butterflies are aimed to study at the same time, then tracking individuals may be an appropriate sampling method. However, it requires a strict protocol and demands huge labour efforts. It is inevitably necessary to avoid influencing the behaviour of butterflies during their observation by keeping a minimum distance from them. In **Study III**, we tracked randomly chosen females. Each landing point of the butterflies was marked and their behaviour was recorded in detail. At the end of the observations butterflies were captured, marked and released to avoid their repeated sampling and the distance and direction between consecutive landing points were measured. The number of eggs laid by the females during the observation was also recorded. At the same time a MRR sampling was carried out to estimate female survival rate.

Detailed description of applied sampling methods are provided in our publications and references cited therein.

Data analysis

MRR datasets were often used to estimate parameters of population dynamics, however it formed only a minor part of our work presented here. The steps of the analysis were in the following order: first we checked whether the dataset fitted the Cormack–Jolly–Seber (CJS) model using a bootstrap GOF test. The CJS model includes two parameters: (apparent) survival rate (φ) and capture probability (p) both of which may be time-dependent and

different between sexes. The best parameter options were found by a model selection procedure based on AIC_c values and the estimations of this model were accepted.

In some studies, spatial distribution of butterflies and environmental variables was characterized by Moran's I index of spatial autocorrelation (Moran 1948). This statistics was also used to detect any spatial autocorrelation in the residuals of generalized linear models.

Generalized linear mixed models provide a flexible approach for analyzing nonnormal data that involve random effects, which are frequently obtained in ecological studies. Nonnormal data often come from count data (such as transect counts) that should be handled by using link functions and exponential family (e.g. normal, Poisson or binomial) distributions (Bolker et al. 2009). If we have a hierarchical sampling design, random effects may encompass the variation within and among the different levels. We applied this method in all studies.

Movement data were obtained by different sampling methods and had different structure. In **Study II**, each recapture was considered as a move which could be characterized by a length and duration. Moves were classified into two groups by that the marking and recapture had happened in the same sampling unit (*residents*) or in different ones (*emigrants*). Distribution of the time length between the two captures in these two groups were compared by Wilcoxon rank-sum test. The distribution of move lengths of emigrants were compared between sexes and species using the same statistics. On the other hand, in tracking studies (**Study III**) high number of moves (15–30) were recorded for each butterfly, albeit fewer individuals were sampled. Flight paths can be approximated by a series of connected straight line moves between the consecutive landing points. Analysis was based on the random walk approach, which assumes that consecutive move lengths and turning angles are not correlated. The test of the random walk model involved special simulation techniques and was done on a case-by-case basis (e.g. Turchin 1998; Schtickzelle & Baguette 2003b).

More details on the methods of data analysis can be found in our selected papers and references cited therein.

RESULTS

The most important results of each publication are summarized here. For further details, figures and tables please see the papers in the Appendix.

Edge type effect was significant for both *M. teleius* and *M. nausithous* in **Study I**, however, the effects were contrasting. Density of *M. teleius* was higher in road transects than in tree transects, while *M. nausithous* was more prevalent in tree transects. Edge effect was significant for *M. nausithous* only, which was found in higher densities at edge transects than at interior ones (Figure 2). Regarding the microenvironmental parameters, air temperature was practically equal at all transect types, but we found a significant edge type $\times$ distance from edge interaction for air humidity, which means that the edges were more humid than the interiors at tree edges. Wind speed was significantly lower at tree edges than road edges and edge transects were less windy than interiors at tree edges. Both the edge type and the distance from edge affected the food plant density which was highest at road interiors and lowest at tree edges. We found significant negative correlation between *M. teleius* density and air humidity and a positive correlation with food plant density. In the case of *M. nausithous*, butterfly density was significantly negatively correlated with wind speed and food plant density.

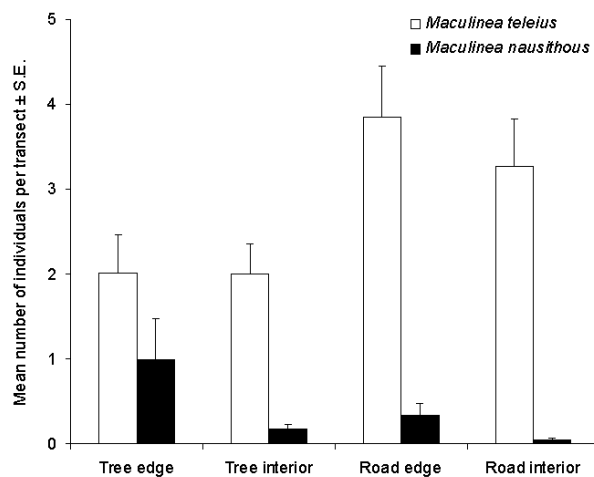


Figure 2. Bars indicate means with SE of number of *M. teleius* and *M. nausithous* per transect count on two types of edges and interiors of meadows.

A total of 171 and 1085 individuals of *M. nausithous* and *M. teleius*, respectively, were marked in **Study II**. Mean abundance of *M. nausithous* in sampling units was 13.7 (range: 1–50, median=10), while that of *M. teleius* was 78.5 (range: 16–171, median=65.5). Global

Moran-tests showed a significant positive spatial autocorrelation for *area* and *forest proportion* of spatial units as well as for *abundance* and *density* of *M. nausithous*. Although the global tests could not identify the exact location of positive spatial autocorrelation, the patterns could be illustrated by maps of the sampling area on which shading indicates the value of each variable (Fig. 3). These maps show that spatial aggregation of *M. nausithous* coincides with high values of *forest proportion* and small values of *area*.

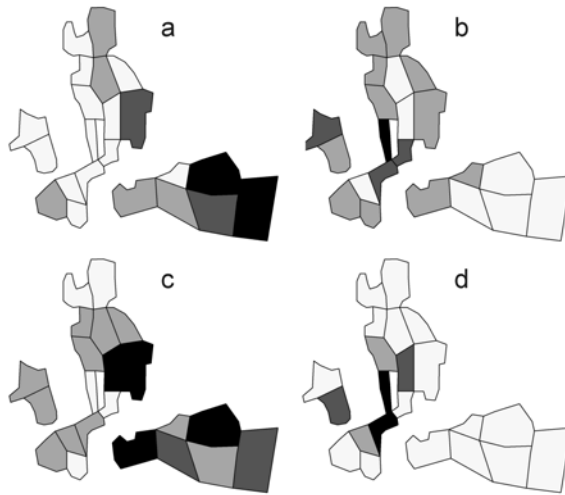


Figure 3. Maps illustrating the distribution and spatial autocorrelation of (a) *area*, (b) *forest proportion*, (c) *abundance* of *M. teleius* and (d) *M. nausithous*. Values are classified in equal intervals. Darker shading indicates higher values.

The area of afforested edge zone (*forest edge*) had not any significant effect on butterflies' density or abundance in any one model. In the case of *M. teleius*, *area* had a significant positive, while *forest proportion* had a significant negative effect on the abundance (Table 3 in **Study II**). None of the predictors had any significant effect on the density of *M. teleius*. Contrarily, both the abundance and density of *M. nausithous* were positively affected by *forest proportion*, but models for density had much higher predictive values (Table 3 in **Study II**). *Area* had a marginally significant effect on abundance and diagnostic plots suggested a weak model fit. However, $\log(\text{area})$ had significant negative effect on density. There were no remarkable differences between sexes in any models.

The emigration rate of *M. teleius* was significantly influenced by all predictors with the exception of *forest proportion* (Table 4 in **Study II**). *Area* and *forest edge* had significant negative effects. *Density of males* also had a negative effect on both males' and females' emigration rate, while *male proportion* affected the emigration rates positively. For the

pooled data, we also found a negative relationship between density and emigration rate. For *M. nausithous*, due to the low number of captures per sampling units the emigration rate could not be modelled.

We recorded 77 moves of *M. nausithous* (males: 51, females: 26) and 483 of *M. teleius* (males: 157, females: 326). The proportion of residents was not different in the two species (χ^2 -test: $\chi^2=0.27$, $p=0.61$) nor between sexes for each species (χ^2 -test: *M. nausithous* $\chi^2=0.02$, $p=0.89$; *M. teleius* $\chi^2=0$, $p=0.99$). We found no significant differences in the time length between two captures of residents and emigrants, indicating that move length was not time-dependent. Move lengths of females were significantly higher for *M. teleius*, and marginally significantly higher for *M. nausithous*. We found no differences between species. Only two individuals of *M. teleius* took a longer move than 200 m, while the longest move taken by *M. nausithous* was 190 m.

In **Study III**, we could collect movement and behaviour data of 30 females of *M. alcon*. We found that the assumptions of the uncorrelated random walk model were fulfilled as there was no autocorrelation either between consecutive turning angles or move lengths and turning angles were uniformly distributed. Plotting the observed and expected values of net squared displacement against the number of moves provides a test of the fit of the random walk model. We found net squared displacement averaged over all observed paths increased linearly with the number of moves (n) until $n=15$, where it peaked and thereafter it declined. In this declining phase it was much lower than the expected values. It means that on average, the net displacement from the starting point of individual butterflies continuously increased up to the 15th move, but afterwards they tended to return to the vicinity of the starting point.

We simulated 95% confidence intervals of net squared displacement for each number of moves for each path, and the observed values fell below the simulated confidence limit in 13 out of 30 paths, indicating that the random walk model overestimated the net squared displacement. We calculated the ratio of net displacement and cumulative number of moves for each n of each path (as an indicator of movement directionality) and its relationship to the number of moves was significantly negative. It also suggests, that butterflies' movement was restricted.

A total of 72 egg-laying events of 22 females were observed. The median of number of eggs laid at one attempt was 2. We found a significant positive relationship between the duration of observation and the number of eggs laid. The estimated survival rate of females was 0.763 from which the average residence time was calculated at 2.58 days. Combining this with the estimated number of eggs laid per hour we estimated that an average female

lays ~100 eggs. The number of ova counted in some virgin females dissected (mean=375.6) greatly exceeded the number of eggs laid per butterfly.

We also attempted to reveal the oviposition preferences of females by analysing the presence or absence of egg-laying in relation with some characteristics of the plants alighted and their close environment. These results were published in a paper which is not included in the Appendix (Kőrösi et al. 2007). We found no significant predictors for the presence/absence of egg-laying, while the number of eggs laid was negatively influenced by the number of bushes within 3 m and the number of gentian shoots within 3 m. The presence of host ants beneath the food plants had no effect on the number of eggs laid by females. However, these latter results were obtained from regression tree analyses which do not provide significance levels and effect sizes. Briefly, we can conclude that no clear oviposition preferences could be found.

Although three *Maculinea* species occurred in the sampling sites in **Study IV**, we could collect sufficient data for statistical analyses for *M. teleius* only. We found a significant effect of mowing on the abundance of butterflies, which was significantly greater in the quadrats mown in May and mown in May and in September. Similar results were obtained for the number of food plant flowerheads. However, the abundance of *Myrmica* host ants was significantly higher in the unmown control quadrats than in managed ones. In all these models, the random factor explained more than 50% of the variance due to that response variables were significantly different between meadows. In other words, the between-site variance was higher, than between-management variance within sites. When we performed Kruskal–Wallis tests on each meadow separately, we found significant effect of mowing on food plant quantity in two meadows, on butterfly abundance and host ant frequency in one-one meadow. Finally, food plant quantity had no effect on butterfly abundance, while host ant frequency had a marginally significant negative effect.

DISCUSSION

We revealed a number of fundamental characteristics of population structure and habitat use of large blue butterflies in our case studies. Firstly, we found that microdistribution and habitat use are different for two sympatric species of *Maculinea* butterfly both at fine spatial scale and at landscape scale. *M. nausithous* occurred in highest density along the afforested edges of meadows. As a consequence, its distribution was strongly aggregated and forest strips did not seem to hinder its movement. On the other hand, *M. teleius* primarily occupied

the meadow interiors, it showed a quite even distribution and its movement was limited by forests. Moreover, the overall density of *M. teleius* was higher than that of *M. nausithous* on all meadows where they co-occurred (**Study I, II, IV**). The co-occurrence of these species is very common throughout Europe (e.g. Thomas 1984b; Wynhoff 1998a; Nowicki et al. 2007; Dierks & Fischer 2009) indicating that their co-existence is stable. Some authors emphasized that this co-existence is facilitated by the different flowerhead selection for oviposition by the two species (Figurny & Woyciechowski 1998; Thomas & Elmes 2001). However, the most important factor regulating the size of *Maculinea* populations is the availability of a high number of sufficiently large host ant nests near to the food plants (e.g. Hochberg et al. 1992). Host ant specificity of *M. nausithous* and *M. teleius* is different, as *M. nausithous* almost exclusively uses *Myrmica rubra* as a host, while *M. teleius* caterpillars can be successfully reared by several other *Myrmica* species (Sielezniew & Stankiewicz 2008; Tartally & Varga 2008; Tartally et al. 2008; Witek et al. 2008). Therefore, there must be only a minor resource competition (with high variance between populations) between these two butterfly species. Microclimatic requirements of *Myrmica* ants are various, *M. rubra* prefers the most humid and coolest soil conditions and it is the predominant ant species on meadow edges near to forests and may have supercolonies (Elmes et al. 1998; Dauber & Wolters 2004). Therefore, preference toward afforested meadow edges by *M. nausithous* butterflies seems to be adaptive since here the coincidence of host ants and food plants is expected to be higher than elsewhere. *M. teleius* prefers meadow interiors, where ant communities consist of more species, but this butterfly may be reared by several *Myrmica* species (Tartally & Varga 2008, Witek et al. 2008). This low host-specificity assures sufficient food plant–host ant coincidence. Thus the different habitat use and microdistribution of these two *Maculinea* species may be a consequence of their different host ant use, which allows their stable co-existence. Presumably the two species diverged so that in *M. nausithous* there could have been a shift in host ant specificity toward *M. rubra*, which resulted in a preference of adult butterflies to wetter and cooler microclimate (Als et al. 2004).

We stress that the difference in the microdistribution and habitat use of *M. teleius* and *M. nausithous* that we found is such a novelty which has not been published before. Several authors have already investigated the structure and dynamics of sympatric populations of *M. teleius* and *M. nausithous* in Europe, but none of them reported significant quantitative differences in their habitat use (in France: Thomas 1984b; in the Netherlands: Wynhoff 1998b; in Poland: Nowicki et al. 2005, 2007; in Germany: Dierks and Fischer 2009). Some authors found differences in the flowerhead selection for oviposition of the two species, but

no discrepancy in the spatial distribution of adult butterflies was detected (Thomas 1984b; Figurny and Woyciechowski 1998; Thomas and Elmes 2001). Moreover, *M. nausithous* is known to be a more abundant species in Western and Central Europe (Wynhoff 1998a; Dierks & Fischer 2009 and references therein). However, we found that *M. nausithous* had a much narrower niche and therefore much smaller abundance in the study region than *M. teleius*. The latter is a more common and widespread species in whole Hungary as well. This discrepancy between the habitat use of Hungarian and other European populations of the two butterflies can be explained by climatic reasons. Among all localities where sympatric populations of *M. teleius* and *M. nausithous* were studied the annual mean temperature is highest, while annual precipitation is the lowest on the Hungarian sites. The only host ant of *M. nausithous* (*Myrmica rubra*) prefers relatively humid and cool microclimatic conditions, which are likely to be found at the afforested edges of meadows only, therefore we suppose that *M. nausithous* is constrained to stay and oviposit at edges to provide sufficient probability of adoption for the offsprings.

The effect of food plant density on butterfly density was ambiguous in our studies. In **Study IV** we found no correlations between the density of *M. teleius* and its food plant, which is in agreement with the findings of some other studies. The generally accepted view is that food plant quantity is not a limiting factor for this butterfly (Nowicki et al. 2007). However, in **Study I** there was a significant negative correlation between *M. nausithous* and food plant density, while density of *M. teleius* was positively correlated with it, which contradicts to other studies (**Study IV**; Nowicki et al. 2007; Anton et al. 2008), which did not find any relationship between food plant and butterfly density. We suppose that this pattern in **Study I** is simply the result of different within-site distribution of the two butterfly species. *M. teleius* preferred meadow interiors, while *M. nausithous* was more abundant at forest edges and their common food plant (*Sanguisorba officinalis*) was more abundant in meadow interiors, so its distribution overlapped better with the distribution of *M. teleius*. In a different study on *M. teleius* in the Kiskunság National Park Batáry et al. (2007) found a positive correlation between food plant density and butterfly density. Dierks and Fisher (2009) also found some positive relationships between food plant density and density of *M. teleius* and *M. nausithous* in a landscape-scale study in Germany. We highlight that food plant density varied in a wide range in all of the above mentioned studies. When its density is low (~ 5 flowerheads m^{-2} e.g. Batáry et al. 2007; Dierks & Fischer 2009) food plant can be a limiting factor for the butterflies and therefore a positive correlation between food plant and butterfly density can be detected. Above a certain threshold, food plant becomes a non-

limiting factor and other ecological factors may take more important roles. In such cases no relationship between food plant and butterfly density is expected (Nowicki et al. 2007; Anton et al. 2008; **Study IV**). However, in the study of Batáry et al. (2007) the overlap between microhabitat requirements of the food plant and *M. teleius* was high (both were found in largest quantity in the same microhabitat types) providing an alternative explanation for the positive correlation between their densities.

We found a clear negative density–area relationship in *M. nausithous* in **Study II**. This relationship was showed to be a characteristic of butterfly metapopulations by Hambäck & Englund (2005) in a meta-analysis. More specifically, Hanski et al. (1994) revealed this relationship in *Melitaea cinxia* and more recently Nowicki et al. (2007) found a similar pattern in *Maculinea teleius* and *M. nausithous*. The explanations for this pattern are various. Hanski et al. (1994) concluded that negative density–area relationship stems from the fact that larger patches are typically of lower average quality, but they did not elucidate this point further. Bukovinszky et al. (2005) argued, that butterflies use distant visual cues to find suitable food plant patches and so the scaling of immigration rates will become more diameter- than perimeter-dependent. Hambäck & Englund (2005) emphasized, that asymmetric migration (diameter-dependent immigration and perimeter-dependent emigration) may cause a negative density–area relationship. On the other hand, Nowicki et al. (2007) found no spatial autocorrelation in densities of local populations of *Maculinea* butterflies, dispersal was fairly symmetric and did not affect local densities significantly. They hypothesized, that host ants are under strong parasitic pressure in meadow interiors where food plant density is usually high. Therefore, small and internally fragmented patches may have higher densities of host *Myrmica* ants, because patch surroundings could constitute refuge space for them. Contrarily to these studies, we sampled one single population of *M. nausithous* in a heterogeneous habitat patch (**Study II**). In this case, the negative density–area relationship was caused by the aggregation of butterflies in certain small spatial units, which was detected as a significant positive spatial autocorrelation in their density. We suggest, that small units may have higher proportion of afforested edge and thus they were of higher quality for *M. nausithous*.

We demonstrated in **Study II**, that movement of adult butterflies within habitat patches was sex-biased. For *M. teleius*, the emigration rate of both genders was positively influenced by the proportion of males. High proportion of males can decrease their chance to find suitable mating partners and increases male harassment that females suffer from (Baguette et al. 1996, 1998). To our best knowledge, sex-biased density-dependent movement of

butterflies or male avoidance as a cause of female emigration has been found in a few studies only, and the spatial scale of such studies was much larger than in our present one (Shapiro 1970; Odendaal et al. 1989; Baguette et al. 1996, 1998). Furthermore, we found that the mean distance moved by individuals was higher in females indicating their higher mobility for both *M. teleius* and *M. nausithous*, which is a widely recognized phenomenon in butterflies (e.g. Kuussaari et al. 1996; Petit et al. 2001; Zimmermann et al. 2005). Nevertheless, our results are particularly interesting, because all of the studies cited above were carried out at metapopulation scale, while our study was performed within one single population at a much finer spatial scale.

In some studies we could quantitatively analyze the movement pattern of *Maculinea* butterflies and we revealed that they performed a restricted movement within habitat patches and may have had home ranges. This phenomenon has been rarely investigated and only some long-life tropical butterflies were known to establish home ranges (e.g. Mallet 1986), which is different from the territorial behaviour of males detected in many species (e.g. Baker 1972; Bitzer & Shaw 1995; Fischer & Fiedler 2001; Kemp 2002). In **Study II**, mean move length of both studied species was unexpectedly small indicating that the majority of butterflies stayed within smaller parts of the sampling site, which was a small habitat fragment. Moreover, an extremely tiny proportion of individuals took any moves in the range of the largest distances that could have been detected (~240 m). Movements were detected most frequently between neighbouring spatial units. We provide different explanations for this limited within-habitat movement of the two studied species, which has already been demonstrated by Hovestadt and Nowicki (2008). In the case of *M. nausithous*, the lack of relatively long movements may have been due to that the distribution of this species was highly aggregated in some particular spatial units near to forest edges and butterflies were rarely observed in a number of units. On the other hand, *M. teleius* was more evenly distributed throughout the study site, but its movement seemed to be hindered by forest strips. Additionally, the lack of time-dependence in butterflies' move lengths suggests that they did not follow the rules of a pure random walk, which is a widely used null-model for animal movement (e.g. Blackwell 1997). However, this analysis was not a thorough test of the appropriateness of the random walk model (see Hovestadt & Nowicki 2008).

In **Study III**, we clearly demonstrated that the random walk model was not appropriate for characterizing the within-habitat movement of *M. rebeli* females, since it overestimated the net displacement. All approaches applied in our analyses suggested that the movement of butterflies was restricted and that they established home ranges. In most studies, within-

habitat movement is assumed to be random (e.g. Odendaal et al. 1989; Schultz & Crone 2001; Ovaskainen 2004), and non-random movement of butterflies has been demonstrated in the matrix and at habitat boundaries only (Conradt et al. 2000; Conradt & Roper 2006). Recently, Hovestadt & Nowicki (2008) found that *M. teleius* may also establish home ranges within habitat patches. The coincidence of their conclusion with ours is notable, because Hovestadt & Nowicki (2008) performed a thorough analysis of a mark–release–recapture dataset, so their results derive from an analysis of patterns (the spatial distribution of individuals), while tracking individuals provided us a deeper insight into the process (movement of individuals) that generates the pattern. Moreover, we were able to combine this process with the spatial distribution of resources. The observed movement pattern departed from that predicted by the risk-spreading hypothesis, but the results do not disprove its other two predictions (Root & Kareiva 1984), because *M. rebeli* females laid eggs singly and very few eggs were laid per plant by a single female.

Our first reason for the restricted movement of females is that even a home range of observed mean size (325 m²) can be enough for a female to avoid sibling competition, if it contains high density of food plants. We can calculate that a *M. rebeli* female's mean home range contains 9.75 exploitable host ant colonies capable of rearing a total of 52 *M. rebeli* larvae to adulthood each year. Combining our values of lifetime natality (101 eggs per female) with some published values on larval survival (Hochberg et al. 1992), we obtain a figure of 42–54 pre-adoption larvae per female each year (see calculations in Kőrösi et al. 2008). Moreover, competition between siblings is further reduced due to polymorphic growth of caterpillars: 75% of the cohort take 2 years to develop per host ant nest and 25% take 1 year (Thomas et al. 1998a). As described above, females spread their eggs fairly evenly within their home ranges, thus even as small an area as 325 m² is sufficient to lay the maximum number of eggs in their lifetimes whilst avoiding sibling competition. However, the period of time during which our observations were made was short and we can be sure that females do not spend all of their lives within such small home ranges and they are unlikely to show territorial behaviour, so females' home ranges certainly overlap. Finally, compared to the length of the flight period the lifetime of individual females is short, which ensures that no food plant patch can be monopolized by a single female.

Direct observation of egg-laying allowed us to find another reason for the restricted movement. Even if our estimates of the daily survival rate and the egg-laying rate contain uncertainties, the difference between the egg load and the estimated number of eggs actually laid by a female over its lifetime suggests that egg-laying of *M. rebeli* is time constrained,

which is otherwise a widespread phenomenon among butterflies (Kingsolver 1983; Doak et al. 2006). We argue that time-constrained nature of egg-laying may be another cause of restricted movement. Time limitation increases the costs of flying, since it consumes energy and time also. The benefits for females of greater movement are poor due to the unpredictability of larval survival and the ease with which sibling competition can be reduced. Therefore, restricted movement may result in a higher reproductive output per female. Furthermore, time limitation may explain why we did not find clear oviposition preferences: choosy oviposition would demand much time for the selection of suitable plants, which is costly for a time-constrained butterfly. The lack of effect of the presence of host ants beneath the food plants selected for oviposition indicates that *Maculinea* butterflies are not able to detect host ants, which was previously suggested by Thomas & Elmes (2001).

We stress that in both studies where the movement of *Maculinea* butterflies were found to be restricted the sampling sites were abandoned grasslands. In such habitats, the advance of scrubs and weeds overgrowing the area inevitably causes the internal fragmentation of the habitats, which may be another possible reason for the restricted movement of butterflies as they tend to stay within suitable micro-patches with high density of food plants. Furthermore, the movement pattern of individuals is likely to be affected by population density, but this effect could not be tested in any of our studies.

Despite of the short period of experimental management and small sample size in **Study IV**, we found a significant effect of mowing on the density of *M. teleius*, its food plant and host ants. However, the frequency of *Myrmica* ants was affected negatively by mowing, while butterfly and host plant density were enhanced by increasing mowing frequency. A possible explanation for this pattern can be that mowing in May favours the growth of the host plant which can reach a larger coverage by the time of the butterfly's flight period (July–August). Higher density of host plants may be attractive for female butterflies and it is likely that the density of eggs laid is higher. This means a higher parasitic pressure for host ant colonies, which can be seriously damaged or weakened by *Maculinea* caterpillars. The infected host ant colonies become less competitive and can be superseded by other ant species (Elmes et al. 1998). In other words, there is an apparent competition between the food plant and host ants of *Maculinea* butterflies, as food plants transmit the parasitic caterpillars to the ant colonies (Thomas et al. 1997). Food plant coverage is lower on less intensively mown areas which may serve as refugia for *Myrmica* ants. Alternatively, microclimatic conditions can be less favourable for *Myrmica* ants in more intensively managed parts of the habitat. Should any one of these explanations be correct, our results call

the attention to the fact that mowing has a contrasting effect on the two main resources of *Maculinea* butterflies. Therefore, future management schemes of *Maculinea* habitats should involve the maintenance of a mosaic-like landscape, where high density food plant patches and refuge areas for host ants form a fine-grained habitat complex.

In spite of the evident differences among sampling meadows regarding their management history and vegetation structure, the effect of mowing was not ambiguous on them. The random factor reached a high value in all mixed models which indicates that there may have been larger differences in the response variables between the meadows than between different managements within the meadows. This fact clearly supports the general idea derived from modelling studies that conservation acts for *Maculinea* habitats must be designed and realized on a case-by-case basis (Mouquet et al. 2005b). As habitat management is a key factor in the long-term preservation of *Maculinea* butterflies (e.g. Johst et al. 2006), we intend to continue the monitoring of the effects of different management types.

Although most of our studies were carried out at the spatial scale of local populations, the results support the view that *Maculinea* butterflies usually do not form classical metapopulations (see Nowicki et al. 2007). Instead, the restricted within-habitat movement and the non-homogeneous distribution of butterflies suggest that *Maculinea* species exist in patchy populations. In these populations we managed to reveal several patterns which had been previously found only in butterfly metapopulations at the landscape scale. The mechanisms underlying these patterns can be various, such as establishment of home ranges or very specific habitat preferences (e.g. *M. nausithous*). The latter draws attention to that habitat patches which seem to be homogeneous for human observers (such as large food plant patches) may be perceived as non-homogeneous by butterflies and their presence and movement can be constrained to certain sub-regions of the habitat. The reason is that food plant is not the only resource butterflies require and therefore biotopes or vegetation stands are not equal to habitats. The overlap of several resources is needed to define a bounded space as a habitat. Instead of the prevailing patch vs. matrix view, we support the idea that a resource-based concept of butterfly habitats would be straightforward to understand their ecology and more effective in practical conservation (Dennis et al. 2003, 2006). The simplistic view of patch vs. matrix can be dangerous, because it takes into consideration the size and isolation of habitat patches only, but neglects the quality of habitats, which is otherwise recognised as a very important factor in the persistence of butterfly populations (e.g. Dennis & Eales 1999; Fleishman et al. 2001; Thomas et al. 2001).

To summarize the implications of our results for the conservation of large blue butterflies we stress that, despite the apparent similarity of their ecological requirements, we succeeded to reveal a contrasting habitat use between two closely related *Maculinea* species inhabiting the same habitats and using the same food plant. This result has serious consequences for the definition and management of the habitats of the two species in the future. Additionally, we found that movement of *Maculinea* butterflies within habitat patches can be restricted, which may lead to an internal fragmentation of local populations. Finally, we tested the effects of different mowing types on the density of *M. teleius* and its resources, which is otherwise unprecedented, and based on our preliminary results we envisaged some fundamentals of a management scheme for the habitats of large blue butterflies in the Órség National Park.

SUMMARY

Butterflies have become frequently used model organisms in biology, especially in population ecology. They have played a disproportionate role in the advance of metapopulation theory, which is one of the most successful attempts in ecology to incorporate the effects of space into population processes explicitly. Uniquely among European butterflies, *Maculinea* species are obligate social parasites of *Myrmica* ants. This special life cycle has attracted the attention of many researchers, while the extinctions or rapid decline of their populations throughout W Europe made a lion of them and nowadays they are ‘flagship’ species for European nature conservation.

A huge amount of data has been collected and a sound knowledge base built up about the biological interactions between *Maculinea* butterflies, their food plants, host ants and parasitoids in the past decades, but quite a few studies investigated the demographic processes in populations and the habitat use of adult butterflies. According to these studies, *Maculinea* butterflies do not form classical metapopulations, because they occupy almost all available food plant patches, local population sizes are stable and interpatch movements are quite rare. Thus no colonization-extinction dynamics occur in *Maculinea* populations and local population processes are supposed to have a major influence on long-term persistence of these species.

At the same time, several authors suggested that the biology of species and behaviour of individuals may have influence on metapopulation dynamics and thus should not be ignored. Metapopulation theory is thought to be simplistic having some assumptions that are

biologically unrealistic in many cases. For example, the patch vs. matrix view of the habitat considers habitat quality as a binary variable (0 or 1), although habitat quality is known to be a highly influential factor in the persistence of many butterfly species. Furthermore, the spatial delineation of habitat patches can not be unambiguous for many butterflies, as their resources are not patchily distributed. In addition, metapopulation models and a number of earlier studies assumed (but rarely tested) that butterflies' movement follows a correlated random walk (both within and outside habitat). However, some recent studies suggested that within-habitat movement of *Maculinea* species can be limited and butterflies may establish home ranges.

Therefore, we studied the microdistribution, habitat use and movement pattern of *Maculinea* butterflies at the level of single populations. Firstly, we investigated how the density of *Maculinea nausithous* and *M. teleius* was influenced by edge types and distance from edges on meadows where they co-occur. These species use a common larval food plant, the great burnet (*Sanguisorba officinalis*), and their flight period entirely overlaps in the Őrség region, where our study was carried out. We designated two pairs of transects on each of ten meadows along the Szentgyörgyvölgyi stream. One pair was laid at an afforested edge of the meadows (tree edge): one transect directly next to the trees and the other one 15 m further inside parallel to the edge transect. Another transect pair was laid down in the same way at the so-called road edge next to a narrow paved or unpaved road with no trees or bushes and very low traffic. The number of butterflies was detected by walking along the transects once everyday during the peak of flight period. We found a contrasting effect of edge type on the two species. Density of *M. teleius* was higher in road transects than in tree transects, while *M. nausithous* was more prevalent in tree transects. Edge effect was significant for *M. nausithous* only, which was found in higher densities at edge transects than at interior ones. The microenvironmental parameters, especially air humidity and wind speed were different on different edges. Both the edge type and the distance from edge affected the food plant density which was highest at road interiors and lowest at tree edges. We found significant negative correlation between *M. teleius* density and air humidity and a positive correlation with food plant density. In the case of *M. nausithous*, butterfly density was significantly negatively correlated with wind speed.

We attempted to reveal some differences in the habitat use and microdistribution of *Maculinea nausithous* and *M. teleius* within one single habitat fragment where they co-occured. We carried out a detailed mark–release–recapture study on the sampling site divided into 22 spatial units. We found the density of *M. nausithous* significantly positively

autocorrelated, while *M. teleius* was more evenly distributed. The proportion of afforested unit edge had a positive effect on *M. nausithous* density, but it had no influence on *M. teleius*. There was a significant negative density–area relationship for *M. nausithous*. Coverage of afforested unit edge had a negative effect on the emigration rate of *M. teleius*. Movement was sex-biased for *M. teleius*, as both males and females tended to emigrate from units with high proportion of males. The mean length of observed movements was surprisingly small for both species and we rarely detected any moves between the farthest parts of the sampling site, indicating that movement of butterflies was restricted to smaller sub-regions of the site. Female mobility was higher than that of males for both species but we found no differences between the mean move length of the two species.

These results clearly proved that microdistribution and habitat use were different for the two species both at single patch and at landscape scale. This may be a consequence of that the primary resource (the host ant) of the two species is different, which otherwise allows their stable co-existence. The only host ant of *M. nausithous* (*Myrmica rubra*) prefers the coolest and most humid microclimate and it is the predominant ant species on afforested edges of meadows. Thus the preference of *M. nausithous* for these edges is adaptive, since there the host ant–food plant coincidence is higher than elsewhere. On the other hand, *M. teleius* uses several *Myrmica* species as hosts and this butterfly primarily occupied the meadow interiors, where ant communities consist of more species. In addition, we demonstrated several phenomena in these populations (negative density–area relationship, sex-biased movement, aggregated distribution and restricted movement) which had been known previously from studies on butterfly metapopulations at landscape scale. Moreover, we provided some arguments to change the prevailing patch vs. matrix view of habitat and supported the use of a resource-based concept for habitat definition.

We aimed to clarify whether within-habitat movement of *Maculinea* species can be described as a random walk and their egg-laying is time- or egg-constrained. We hypothesized, that *M. alcon* females are not able to predict the survival of their offsprings at the moment of oviposition, since the most important mortality factor of caterpillars stems from the lack of adoption by host ants and adult butterflies are assumed to be unable to detect the presence of host ants beneath the food plants. Therefore, we expected that female butterflies would apply a bet-hedging strategy and would follow linear flight paths to maximize the net displacement and spread their eggs as widely as possible. We followed 30 randomly selected females of *M. alcon* within a small habitat fragment and recorded their movement pattern and oviposition behaviour. In addition, a mark–release–recapture study

was carried out to estimate the survival rate of females and four non-mated virgin females were dissected to count the load of potential eggs. We found that butterflies' movement was restricted as the maximum net displacement from the starting point was (on average) <20 m. The random walk model was inappropriate for characterizing the movement pattern as it overestimated the net displacement. All approaches applied in our analyses suggested that female *M. alcon* butterflies may have established home ranges (on average 325 m^2). However, it did not disprove the risk-spreading hypothesis, because we revealed that such small home ranges can be sufficient for the females to spread all of their eggs and reduce the competition between their siblings. We estimated the egg-laying rate (~ 5 eggs/hour) and the average lifespan (~ 2.5 day) of females and calculated that an average female can lay approximately 100 eggs during her lifespan, which was much lower than the mean egg load found in dissected females (~ 375 eggs). Thus, the egg-laying of *M. rebeli* is time-constrained, which may be another reason for the restricted movement: flying is costly as it needs energy and time effort but the benefits are uncertain, because the females can not predict the survival of the offsprings. This may be the explanation for that we did not find any clear oviposition preferences of females, since choosy oviposition would be (time) costly and the benefits are questionable.

We started a long-term management experiment to find the most favourable mowing type for the maintenance of the habitats of *Maculinea teleius*. Four mowing types were applied on each of four meadows. We found that higher mowing intensity increased the density of butterflies and food plants, but it had a negative effect on the frequency of host ants. We suppose that there is an apparent competition between food plant and host ants as food plants transmit the parasitic caterpillars to the ant nests, which are seriously damaged by the parasitism. Its consequence is that those areas, which are less favourable for the food plant and for egg-laying females may serve as refugia for the host ants. Alternatively, intensive mowing may change the microclimatic conditions in a manner which is unfavourable for *Myrmica* ants. These results suggest that future management schemes should take into consideration that long-term persistence of *Maculinea* butterflies is most likely in a mosaic-like habitat complex. However, we found remarkable differences between the meadows regarding the food plant and host ant density, which highlights that conservation planning of *Maculinea* butterflies should be performed on a case-by-case basis.

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ÖSSZEFOGLALÁS

A nappali lepkék kitüntetett szerepet játszanak a különféle biológiai kutatásokban és mára modell fajokká váltak számos tudományterületen, mint például az evolúciós ökológiában, a filogenetikában, a populációökológiában és a természetvédelmi biológiában. Ennek oka, hogy esztétikus megjelenésük és viszonylag könnyű megfigyelhetőségük évszázadok óta vonzza a természetbúvárok figyelmét, s ennek köszönhetően napjainkra tekintélyes tudásanyag áll rendelkezésre a lepkék taxonómiáját, elterjedését, ökológiai igényeit, sőt az utóbbi évtizedekben tapasztalható állományváltozásait tekintve is. Nem véletlen, hogy a térbeli ökológia területén kiemelkedő metapopulációs elmélet kidolgozásában is központi szerepet játszottak a nappali lepkék. A térbeliség szerepe az ökológiai mintázatokban és folyamatokban nagy hangsúlyt kapott az utóbbi évtizedekben, és ebben a témában az egyik legdinamikusabban fejlődő elmélet a metapopulációk működésével foglalkozik.

A klasszikus metapopulációs megközelítésben egy adott faj számára alkalmas élőhelyfoltok egy a megtelepedésre alkalmatlan mátrixba ágyazódnak be. Az élőhelyfoltokon élő populációk belső dinamikája egymástól nagyrészt független, köztük a kapcsolatot a diszperzió tartja fenn, melynek révén az élőlény képes megtelepedni a korábban nem elfoglalt területeken is ((re)kolonizáció). A helyi populációs folyamatok eredményezhetnek véletlen kihalásokat, melyeket a rekolonizáció tud ellensúlyozni. Ebben az elméletben az extinkció-rekolonizáció dinamikája határozza meg a metapopuláció hosszú távú fennmaradását, s ebben a legnagyobb szerepet a foltok mérete illetve egymástól való izoláltságuk játsza. Számos kiemelkedő eredmény született a metapopulációs elmélettel kapcsolatban, melyeknek konkrét természetvédelmi hasznosítására is sor került. Ugyanakkor több szerző is felhívta a figyelmet arra, hogy az elmélet olyan előfeltevéseken alapul, amely a legtöbb valós populáció esetében nem teljesül, valamint olyan egyszerűsítéseket tartalmaz, amelyek komolyan befolyásolhatják a modell jóslatainak érvényességét. Sok faj esetében például nem figyelhető meg az extinkciós-rekolonizációs dinamika, mivel ezek a fajok viszonylag stabil populációkat alkotnak és minden potenciális élőhelyfoltot benépesítenek. Továbbá a modell figyelmen kívül hagyja az élőhelyfoltok minőségét, ami pedig a nappali lepkék esetében döntő hatással lehet az ott élő populációk méretére és fennmaradására. Sok faj esetében egyszerűen lehetetlen térbelileg lehatárolni az élőhelyfoltokat, mert az adott faj által használt források eloszlása nem foltszerű, vagy mert a különböző források átfedéseinél változó minőségű élőhelyfoltok jönnek létre, melyek mindegyike szükséges a faj szaporodásához. Egyes szerzők hangsúlyozzák, hogy a mátrix szerepe is döntő lehet a

metapopulációs dinamikában. Végezetül újabban felmerült, hogy az egyedek mozgásmintázata, ami a metapopulációs modellekben véletlenszerűnek van feltételezve, jelentősen eltérhet a véletlen mintázattól (diffúzió), akár szabályos kereső mozgások, akár korlátozott mozgáskörzet formájában.

A hangyaboglárkák (*Maculinea* spp.) (Lepidoptera: Lycaenidae) az Európában honos lepkék között egyedülálló módon obligát szociális parazitái bizonyos *Myrmica* hangya fajoknak. A nőtények a tápnövényre helyezik tojásaikat s a kikelő hernyók néhány hétig a magkezdeményekkel táplálkoznak. Ezt követően a talajra ereszkednek és megvárják, míg bizonyos *Myrmica* fajok dolgozói megtalálják és adoptálják őket. Az adoptáció után a hangyák a fészükbe cipelik a hernyókat. A hangyafészken belül a *Maculinea* hernyók vagy a hangyalárvákat fogyasztják, vagy a hangyalárvákat utánozva elérik, hogy a dolgozók inkább őket etessék. A hernyók kutikuláján található vegyületek (főképp szénhidrátok) nagyfokú hasonlóságot mutatnak a hangyák kémiai kommunikációjában használtakéval, ezért a hangyák a fészkekhez tartozónak ismerik fel a lepke hernyókat. A *Maculinea* fajok gazdaspecifitása fajonként eltérő, egyes fajok (pl. *M. nausithous*) kizárólag egy *Myrmica* faj fészkében élőködnek, míg más fajok több gazda fajt is használhatnak. A *Maculinea* hernyók testtömeggyarapodásuknak 99%-át a hangyafészkekben érik el, itt telnek, itt bábozódnak és az imágók innen kelnek ki. A lepkék számára a hangyákkal való kapcsolat obligát, vagyis adoptáció hiányában a hernyók életképtelenek. A hangyakolóniák számára a lepke parazitikus viselkedése komoly reprodukciós hátrányt okozhat.

Egyedülálló életmenetükön kívül az irányította a figyelmet a hangyaboglárkákra, hogy állományaik Nyugat-Európában az utóbbi évtizedekben látványosan megfogyatkoztak, számos országban kipusztultak a védelmi intézkedések ellenére (pl. Anglia, Hollandia). Éppen ezért a legtöbb európai országban védettek, a Natura2000 Élőhely Irányelvek függelékeiben is szerepelnek. A kutatások bebizonyították, hogy a hangyaboglárkák rendkívül jó indikátor fajok, mivel igen érzékenyen reagálnak az élőhelyüket ért kedvezőtlen változásokra. Emellett ernyő-fajokként is szolgálhatnak, hiszen élőhelyük megóvásával számos más élőlény számára teremthetünk lehetőséget a fennmaradásra és olyan élőhelytípusok maradhatnak fenn, melyek az európai tájakban egyre kisebb arányban találhatók meg. Mindezek miatt a *Maculinea* fajok napjainkra az európai természetvédelem számára „zászlóshajó” fajokká váltak.

A metapopulációs vizsgálatok fent említett hiányosságait figyelembe véve doktori munkámban arra kerestem a választ, hogy milyen mintázatok mutathatók ki a hangyaboglárkák lokális populációin belül a lepkék térbeli eloszlásában illetve

élőhelyhasználatában, továbbá a megfigyelt mintázatokat milyen egyedi szintű mechanizmusok idézik elő. Emellett a hangyaboglárkák hosszú távú fennmaradását elősegítő élőhelykezelési módszerek kiválasztása is szerepelt a vizsgálatok céljai között.

Az Őrségi Nemzeti Park területén két olyan vizsgálatot végeztünk, melyekben a sötétaljú hangyaboglárka (*M. nausithous*) és a vérfű hangyaboglárka (*M. teleius*) élőhelyhasználatát és térbeli eloszlását tanulmányoztuk egyrészt tájleptéken, másrészt egy helyi populáció szintjén. A két vizsgált faj hazánkban olyan nedves kaszálóréteken ill. kékperjés lápréteken fordul elő, ahol lárvális tápnövényük, az őszi vérfű (*Sanguisorba officinalis*) nagy mennyiségben megtalálható. Mindkét faj a vérfű virágzatába helyezi tojásait, repülési idejük pedig teljesen átfed. Emellett sok területen szemmel láthatóan stabilan együttélő populációkat alkotnak. Az első vizsgálatban a Szentgyörgyvölgyi patak mentén 10 réten jelöltünk ki rétenként két transzekt párt. A transztek 50 m hosszúak és 5 m szélesek voltak. Az egyik transzekt párt a rét erdővel határos szegélyében helyeztük el oly módon, hogy az egyik transzekt éppen a szegélyre esett, míg a másik 15 méterrel beljebb a rét belseje felé. A másik transzekt párt ugyanilyen módon a rétnak egy olyan szegélyén jelöltük ki, ahol valamilyen kisforgalmú út határolta a rétet. A legtöbb esetben az út túloldalán szintén a vizsgált fajok számára alkalmas élőhely volt található. A rajzási időszak csúcán naponta egyszer végigjártuk az összes transzektet és mindkét faj egyedeinek számát feljegyeztük, elvégeztük bizonyos időjárási paraméterek mérését, valamint összesen egy alkalommal a tápnövény hajtásokat is megszámláltuk. Eredményeink azt mutatták, hogy a *M. nausithous* denzitására szignifikáns hatással volt a szegély típusa (az erdős szegélyeken nagyobb denzitás), illetve a transzekt helyzete is (a szegély transzекten nagyobb denzitás, mint a belső transzекten). A *M. teleius* esetében csak a szegély típusa volt szignifikáns hatással, a lepkék denzitása az út melletti transzekt páron volt magasabb. A tápnövény denzitására mind a transzekt típusa, mind pedig a transzekt helyzete szignifikáns hatással volt. A legkevesebb tápnövényt az erdős szegélyeken, a legtöbbet az út melletti belső transzекten találtuk. Az időjárási paraméterek közül a szél erősség és a páratartalom mutatott szignifikáns különbségeket. A relatív páratartalom az erdős szegély transzекteken magasabb volt, mint az út mellett, továbbá az erdők mellett a szegélyeken magasabb volt, mint a belső transzекten. Végül a szél erősség az erdős szegély transzекten volt a legalacsonyabb. Összességében tehát a két *Maculinea* faj eloszlása a réteken különböző volt. A *M. nausithous* leginkább a párásabb, kevésbé szeles erdős szegélyeken fordult elő, míg a *M. teleius* az utak melletti belső transzекteken, ahol a tápnövény denzitása a legmagasabb volt.

Második vizsgálatunkban egy populáción belül vizsgáltuk a két faj eloszlását és élőhelyhasználatát intenzív jelölés-visszafogásos módszerrel. Fő kérdésünk az volt, hogy miképpen befolyásolja az erdős szegélyek közelsége ill. aránya a két faj eloszlását és mozgásmintázatát. A mintavételi terület egy kéthektáros, felhagyott nedves kaszálórét volt Kercaszomor mellett, az Őrségi Nemzeti Park területén. A kaszálás hiányában bekövetkező cserjésedés és beerdősülés nyomán a rét négy kisebb foltra tagolódott, ezeket összesen 22 kisebb (300–2200 m²), szabálytalan alakú térbeli mintavételi egységre osztottuk. A jelölés-visszafogást úgy végeztük, hogy minden térbeli egységben annak területével arányos időt töltöttünk, így módon standardizálva a mintavételi ráfordítást. A naponta fogott lepkék számának összegét elosztva a mintavételi egységek területével jellemeztük minden egységben a két faj denzitását. Összesen 171 egyedet jelöltünk meg a *M. nausithous* és 1085 egyedet a *M. teleius* esetében. A *M. teleius* egyedszámát a mintavételi egységek mérete pozitívan, az erdős szegély aránya pedig negatívan befolyásolta, ám e két magyarázó változó között szignifikáns negatív korreláció volt. A *M. nausithous*-nál mind az egyedszámról, mind a denzitásra szignifikáns pozitív hatással volt az erdős szegélyek aránya, míg a mintavételi egységek területe szignifikánsan negatívan hatott. A *M. nausithous* denzitása szignifikáns pozitív autokorrelációt mutatott, míg a *M. teleius* denzitásában nem volt kimutatható autokorreláció.

Minden egyes visszafogási esemény egyúttal egy elmozdulásként is értelmezhető volt, ezáltal lehetővé vált a kivándorlási ráta kiszámítása az egyes mintavételi egységekre, továbbá az elmozdulások hosszának megállapítása. A *M. teleius* esetében a kivándorlási rátát negatívan befolyásolta a mintavételi egységek területe, az erdős szegélyek mérete, valamint a lepkék denzitása. A hímek aránya viszont pozitív hatással volt mind a hímek, mind pedig a nőstények kivándorlási rátájára. A *M. nausithous* esetében az alacsony fogásszám miatt nem tudtuk a kivándorlási rátát modellezni. Az elmozdulások átlagos hossza mindkét faj esetében meglepően alacsony volt (~60–70 m) és csak elvétve figyeltünk meg átmozgást a mintavételi terület legtávolabbi pontjai között (~240 m). A két faj között nem találtunk szignifikáns eltérést, viszont mindkét faj esetében a nőstények elmozdulásai szignifikánsan hosszabbak voltak.

A két vizsgálat eredményei alapján megállapítható, hogy a *M. nausithous* és *M. teleius* élőhelyhasználatuk mind tájleptéken, mind pedig egy adott élőhely-fragmentum esetében különböző. A *M. nausithous* nagyobb denzitásban fordult elő az erdős szegélyekhez közel, eloszlása ennek következtében aggregált volt, míg a *M. teleius* inkább a rétek belső részein fordult elő és eloszlása egyenletesebb volt. Feltételezésünk szerint az eltérő élőhelyhasználat

magyarázata abban rejlik, hogy a két faj legfontosabb forrása, a gazda hangya faj térbeli előfordulása eltérő. (Valószínűleg ez teszi lehetővé stabil együttélésüket.) A *M. nausithous* kizárólag a *Myrmica rubra* fészkeit parazitálja, amely leginkább a nedves, hűvösebb mikroklimatikus körülményeket kedveli, ezért a rétek erdős szegélye mentén domináns faj lehet (ráadásul gyakran képez úgynevezett szuperkolóniákat). Így a *M. nausithous* nőstények számára adaptív stratégia lehet az erdős szegélyek mentén keresni tojásrakó helyeket, hiszen a tápnövény–gazda hangya átfedés mértéke valószínűleg itt a legmagasabb. A *M. teleius* nem ennyire gazdaspecifikus, hernyói legtöbbször a *Myrmica scabrinodis* fészkeiben fejlődnek, de számos más *Myrmica* faj is szolgálhat számára gazdaként (pl. *M. gallienii*, *M. rubra*, *M. salina*). Ezáltal a rétek belsejében, ahol a *Myrmica* közösség fajszáma magasabb, mint a szegélyekben, a *M. teleius* számára megnő az esély arra, hogy a tápnövényt elhagyó hernyókat gazda hangyák adoptálják. Az erdős szegélyek magas aránya a *M. teleius* mozgását akadályozta, míg a *M. nausithous* mozgására nem volt kimutatható hatással, ami kiemeli az erdős szegélyek szerepét a két faj térbeli elkülönülésében.

Emellett a második vizsgálatban számos olyan mintázatot találtunk a lepkék eloszlásában és mozgásmintázatában, amelyeket korábban csak metapopulációs léptékű vizsgálatokban mutattak ki. Ilyen például a negatív denzitás–terület összefüggés, amelyet a *M. nausithous* esetében találtunk, s amely sok más tanulmány szerint jellemző a nappali lepkék metapopulációira, többek között az általunk vizsgált fajokéra is. Szintén metapopulációs vizsgálatokból ismert tény, hogy a nőstények elkerülik azokat az élőhelyfoltokat, ahol a hímek denzitása magas, ugyanakkor a hímek keresik azokat a foltokat, ahol a nőstények nagy egyedsűrűségben fordulnak elő. Ez a mi vizsgálatunkban abban nyilvánult meg, hogy azokból a mintavételi egységekből, ahol a hímek aránya magas volt, onnan mindkét ivar egyedei nagyobb valószínűséggel vándoroltak el. Ez feltehetően annak következménye, hogy a hímek magas aránya a nőstények számára kedvezőtlen gyakori zaklatással jár, mely elől a nőstények megpróbálnak kitérni. Ugyanakkor a hímek közötti kompetíció a fogékony nőstényekért szintén nagyfokú, ezért a hímek is a kivándorlást választhatják. Emellett mindkét faj esetében azt találtuk, hogy a 200 méternél hosszabb elmozdulások gyakorisága rendkívül alacsony volt, továbbá semmilyen összefüggés nem volt az elmozdulások hossza és időtartama között. Mindezek alapján arra következtetünk, hogy a *M. teleius* és a *M. nausithous* mozgása az élőhelyfolton belül erősen korlátozott, aminek fontos elméleti és természetvédelmi következményei lehetnek.

Harmadik vizsgálatunkban a *Maculinea rebeli* (a *M. alcon* szárazréti ökotípusa) nőstényeinek nyomonkövetésével, mozgásmintázatuk és tojásrakásuk közvetlen

megfigyelésével próbáltunk meg két hipotézist tesztelni. A „kockázatmegosztó” hipotézis esetén abból a feltevésből indultunk ki, hogy a nőtények nem képesek utódaik túlélését megjósolni, mivel annak térbeli varianciája magas. Az utódok túlélését ugyanis leginkább az határozza meg, hogy a tápnövényt elhagyó hernyót adoptálják-e a gazda hangyák, a nőtények viszont nem képesek megállapítani, hogy egy adott tápnövény beleesik-e valamely gazda hangyafészek mozgáskörzetébe. A hipotézis ilyen esetekben azt jósolja, hogy a tojásrakó nőtények lineáris útvonalat fognak követni, hogy maximalizálják a bejárt területet és így tojásaikat minél nagyobb területen szórják szét (kockázatmegosztás), ezért mozgásmintázatuk el fog térni a véletlen bolyongás modell által jósoltaktól. Emellett egy tápnövényre várhatóan csak kevés tojást fognak rakni és sok alkalmasnak tűnő tápnövényt figyelmen kívül hagynak. Korábbi vizsgálatok a hangyaboglárkák élőhelyfolton belüli mozgását korlátozottnak találták, ezért alternatív hipotézisünk az volt, hogy a nőtények saját home range-et (mozgáskörzetet) tartanak.

Összesen 30 random módon kiválasztott nőtényt figyeltünk meg Vérteskozma mellett egy ~0,8 hektáros réten, melyet minden oldalról erdő vett körül. A lepkék leszállási pontjait megjelöltük, a leszállási ponton mutatott viselkedést és annak időtartamát rögzítettük, a lerakott tojásokat megszámláltuk. A nyomon követés végeztével a lepkéket megjelöltük, elkerülendő az ismételt megfigyelést, a leszállási pontok közötti távolságot és irányt lemértük. A nyomon követések átlagos időtartama 50 perc volt. Emellett végeztünk a populáción egy jelölés-visszafogás vizsgálatot, hogy a nőtények túlélési rátáját megbecsüljük. Végül négy frissen kikelt, szűz nőtényt felboncoltunk és megszámláltuk a bennük található tojásokat.

A lepkék mozgásmintázata különbözött a véletlen bolyongás (random walk) modelljétől, mivel a nettó elmozdulás négyzetének modell által becsült értékei a megfigyelt értékeknél szignifikánsan nagyobbak voltak. Ez abból adódott, hogy a lepkék által megtett nettó távolság körülbelül a 15. elmozdulásig növekedett, utána viszont csökkent. Ez azt jelenti, hogy átlagosan a 15. elmozdulásnál a lepkék elérték a kiindulási ponttól mért legnagyobb távolságot, majd ezt követően közeledtek a kiindulási ponthoz. Ezek az eredmények tehát egyértelműen a mozgáskörzet hipotézist támasztják alá. A lepkék átlagos mozgáskörzete 325 m² volt, ami feltűnően alacsony, még egy ilyen viszonylag kis területű élőhelyfolton is. A nőtények által lerakott tojások száma egyenes arányban állt a megfigyelés időtartamával, és így megbecsülhettük a nőtények tojásrakási rátáját (~5 tojás/óra). A jelölés-visszafogás adatok alapján pedig a nőtények átlagos élettartamát tudtuk megbecsülni (~2,5 nap), s a két becslést kombinálva megkaptuk egy átlagos egyed élete során lerakható tojások számát (101

tojás). Ehhez képest a kiboncolt nőstényekben átlagosan ~375 megtermékenyítetlen petesejtet találtunk s ebből azt a következtetést vontuk le, hogy a lepkék tojásrakása idő-limitált.

A kockázat-megosztó hipotézisnek a mozgásmintázatra vonatkozó predikciója nem igazolódott be, mert a lepkék mozgása korlátozott volt, ugyanakkor a másik két predikciót a megfigyeléseink igazolták, hiszen a nőstények egy tápnövényre csak átlagosan 2 tojást raktak. Továbbá a gazda hangyák előfordulási gyakoriságáról és a *Maculinea* hernyók mortalitásáról korábban publikált adatok alapján kiszámítottuk, hogy egy 325 m²-es mozgáskörzet is elegendő egy nőstény számára, hogy összes tojását lerakja és utódai között a kompetíciót minimálisra csökkentse, ha a tápnövény elegendő mennyiségben van jelen, ami magyarázatot adhat a korlátozott mozgásra. Természetesen nem állítjuk, hogy a nőstények egész életüket egy ilyen kicsi területen töltik, továbbá a lepkéknek a rajzás időtartamához képest rövid életideje és a territorialitás hiánya miatt a mozgáskörzetek nagy mértékben átfedhetnek. A nőstények idő-limitáltságából következően a repülésnek súlyos költségei vannak (mind az idő-, mind az energiaráfordítást tekintve), ugyanakkor a nyereségek megkérdőjelezhetőek, hiszen a nőstények nem tudják megjósolni utódaik túlélését, a szükséges források kis területen belül is megtalálhatóak és elegendő varianciát mutatnak a kockázat minél egyenletesebb elosztásához.

A hangyaboglárkák többségében olyan gyepterületeken fordulnak elő, amelyeket az ember hosszú ideje művel valamilyen extenzív formában. Az őrési nedves kaszálóréteken a hagyományos mozaikos, kisparcellás kaszálás (és kisebb részben a legeltetés) volt az, ami az élőhelyek fennmaradását biztosította. Napjainkra azonban az állattartás megszűnésével drasztikusan lecsökkent a széna iránti kereslet, továbbá a nagy táblákban történő gépi kaszálás az élőhelyek homogenizálódásához vezetett. Emellett a kaszálás időzítése is teljesen esetlegessé vált, hiszen a gazdálkodók jobbra a kezelési kényszer miatt végzik csak el a rétek kaszálását. Negyedik vizsgálatunkban az Őrségi Nemzeti Parkkal közösen azt a célt tűztük ki, hogy egy hosszú távú kezelési kísérletben megállapítsuk, hogy a vérfű hangyaboglárka (*M. teleius*) populációi számára milyen kaszálási mód a legkedvezőbb.

A Szentgyörgyvölgyi patak mentén négy réten jelöltünk ki 4–4 kezelési sávot. Igyekeztünk gazdaságilag reális kezelési típusokat választani, melyek a következők: (1) kaszálás májusban, (2) kaszálás szeptemberben, (3) kaszálás májusban és szeptemberben, valamint (4) kaszálás nélküli kontroll. A kaszálás minden esetben géppel történik, a kísérletet 2007 májusában kezdtük. Minden kaszálási sávot felosztottunk 20×20 méteres kvadrátokra, ezeknek a közepén pedig 10×10 méteres kvadrátokat jelöltünk ki. Minden évben a *M. teleius*

repülési időszakában végeztük a mintavételt. A lepkék mintavételezését jelölés-visszafogásos módszerrel végeztük oly módon, hogy egy ember 5 percet töltött mintavétellel egy 20×20 méteres kvadráton belül és az összes kvadrát bejárásra került minden mintavételi napon. A mintavételre a rajzási időszak csúcsán két héten át került sor. Az elemzésekben a kvadrátokban megfogott egyedek számát tekintettük függő változónak. A lepke lárvális tápnövényeként szolgáló őszi vérfű mennyiségének felmérését a 10×10 méteres kvadrátokon belül végeztük. A rajzás során egy alkalommal a virágfejeket megszámláltuk, vagy ahol a vérfű nagy denzitása ezt nem tette lehetővé, ott a hajtásokat számláltuk meg és ezt szoroztuk meg 10 random kiválasztott hajtáson talált virágfejek átlagával. A *Myrmica* hangyák mintavételezése szintén a 10×10 méteres kvadrátokon belül zajlott. Minden kvadrátban négy darab, csalival ellátott műanyag lapot helyeztünk ki a kora reggeli órákban, és a kihelyezést követő fél órában az ott talált *Myrmica* hangyákból későbbi meghatározás céljára néhány példányt alkoholba tettünk.

Eredményeink a 2008 júliusában végzett felmérésre vonatkoznak. A kísérlet megkezdése óta eddig az időpontig a négy kezelési sávban eltérő számú kaszálást végeztek (kontroll: 0, szeptemberi: 1, májusi: 2, májusi és szeptemberi: 3). Az eredmények alapján a kaszálás intenzitása pozitívan hatott mind a lepkék, mind pedig a vérfű denzitására. A májusban ill. a májusban és szeptemberben kaszált kvadrátokban a lepkék és a vérfű denzitása szignifikánsan nagyobb volt, mint a kontroll területeken. Ugyanakkor a gazda *Myrmica* fajok gyakoriságára a kaszálás negatív hatással volt, a kontroll kvadrátokban szignifikánsan nagyobb volt a gyakoriságuk, mint a kezelt területeken. Kiemelendő, hogy a modellekbe random faktorként bevett rét-hatás igen nagy volt, vagyis az összvarianciának több mint 50%-át a rétek közötti variancia magyarázta, és csak kisebb részét a réteken belüli, kezelések közti különbségek. Emellett nem találtunk szignifikáns összefüggést a lepkék denzitása és a vérfű mennyisége között, viszont marginálisan szignifikáns negatív kapcsolat volt a *Myrmica* hangyák gyakorisága és a lepkék denzitása között.

Összességében elmondható, hogy a kis mintaelemszám és a rövid kezelési időszak ellenére sikerült a kezelés hatását kimutatnunk. A kaszálás ellentétes hatással volt a vérfű hangyaboglárka két legfontosabb forrásának, a tápnövénynek és a gazda hangyáknak a mennyiségére. Ennek oka lehet az, hogy a májusi kaszálás kedvez a vérfű növekedésének, ami a lepkék repülési időszakára felnő és dominánssá válik a gyeppen. A vérfűben gazdagabb területeket gyakrabban látogatják a lepkék és feltehetően több tojást raknak ott, így a gazda hangyák fészkeire nagyobb parazita nyomás nehezedik. A tápnövény és a gazda hangya között fennálló látszólagos kompetíció (a parazita hernyókat a tápnövény közvetíti a

hangyafészkek felé) tehát azt eredményezi, hogy a tápnövényben szegényebb területek a hangyák számára refúgiumként szolgálnak. Ezeknek a menedékterületeknek a meglehetősen fontos szerepe a *Maculinea* lepkék hosszú távú fennmaradása szempontjából, ezért a leendő kezelési terveknek egy mozaikos kaszálási rendszer kialakítását kell tartalmazniuk. Alternatív magyarázat lehet az, hogy a kaszálás megváltoztatja a gyepek szerkezetét és ezáltal hatással van a mikroklímára, ami szintén alapvető fontosságú tényező a *Myrmica* fajok ökológiai igényeit tekintve. Mindemellett a rétek között talált nagyfokú variancia azt támasztja alá, hogy az élőhelyek kezelési előtörténete és vegetáció-szerkezete szintén befolyásolhatja a kezelések kimenetelét, ezért az optimális kezelés megválasztásának eseti elbírálás alá kell esnie.

Összegezve tehát a következő új tudományos eredményeket értük el. Két közel rokon, együttesen előforduló hangyaboglárka esetében (*M. nausithous* és *M. teleius*) számos különbséget mutattunk ki az imágók élőhelyhasználatában és térbeli eloszlásában mind tájléptéken, mind pedig egy helyi populáció szintjén s ezeket a különbségeket összefüggésbe hoztuk a két faj stabil együttélését biztosító forrás-felosztásukkal. Olyan mintázatokat mutattunk ki egyetlen populáció vizsgálatakor, amelyek eddig csak metapopulációs léptékű tanulmányokból voltak ismertek. Ilyenek például a negatív denzitás–terület összefüggés, vagy a hímek és nőstények eltérő mozgásmintázata. Bebizonyítottuk, hogy a hangyaboglárkák esetenként mozgáskörzetet tartanak és tojásrakásuk idő-limitált, ami megvilágítja a korlátozott mozgás adaptív értékét. Eredményeink alátámasztják azt a korábbi álláspontot, mely szerint a *Maculinea* lepkék nem alkotnak klasszikus értelemben vett metapopulációkat, hanem inkább úgynevezett foltos populációkban fordulnak elő. Ez megkérdőjelezi a táj korábban uralkodó „élőhely–mátrix” felosztását és az élőhelyeknek egy forrásalapú meghatározását támogatja, továbbá felhívja a figyelmet a *Maculinea* populációk belső fragmentációjának lehetőségére, ami fontos természetvédelmi következményekkel bír. Emellett a lepkék élőhelyfolton belüli mozgásmintázatának feltárása hozzájárulhat bizonyos térbeli populációs modellek továbbfejlesztéséhez. Végezetül élőhelykezelési kísérletünk során megállapítottuk, hogy a kaszálás eltérő hatással lehet a hangyaboglárkák két legfontosabb forrásának, a tápnövénynek és a gazda hangyáknak a mennyiségére, ezért mindenképpen a mozaikos élőhelykezelést tartjuk előnyösnek. Továbbá megállapítottuk, hogy a hangyaboglárka élőhelyek optimális kezelésének megválasztása nagy mértékben esetfüggő.

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APPENDIX

Study I

I

**Species-specific distribution of two sympatric *Maculinea*
butterflies across different meadow edges**

Péter Batáry, Ádám Kőrösi, Noémi Örvössy, Szilvia Kövér, László
Peregovits (2009)

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Species-specific distribution of two sympatric *Maculinea* butterflies across different meadow edges

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Abstract An important consequence of habitat fragmentation is the increase of edge habitats. Environmental factors in the edges are different from those in the interiors, which causes changes in the distribution of plant and animal species. We aimed to study how edges affect the distribution of two butterfly species within meadow fragments. We therefore investigated the effect of distance from edge and edge type (road edge versus tree edge) on two sympatric large blue species (*Maculinea teleius* and *M. nausithous*). Our results showed that edge type had contrasting effects on the two species. *M. teleius* favoured both interiors and road edges, while *M. nausithous* preferred the tree edges. In the case of the latter species a strong positive edge effect was also found. This kind of within-habitat niche segregation is probably related to the different microenvironmental conditions at the edges. Foodplant density did not seem to limit the distribution of these species. Our results suggest that interiors of meadows are important for *M. teleius*, while tree edges maintain the habitats of the regionally rarer butterfly, *M. nausithous*.

Keywords Edge effect · Foodplant · Habitat use · Myrmecophily · Niche segregation

Introduction

Recently the destruction of natural and semi-natural habitats progressed very rapidly (Foley et al. 2005). In addition to being directly destroyed, extensive habitats were disrupted into small, isolated patches, a process known as habitat fragmentation (Saunders et al. 1991; Meffe and Carroll 1994; Tscharntke et al. 2002). The decrease in the extent of suitable habitats infers directly the decrease in populations due to the lack or lower availability of critical resources. However, the harmful effects of habitat destruction are not restricted only to the given area of the habitat. Even the loss of a relatively small part of the habitat could hinder the free movement or migration of species (Standovár and Primack 2001). An important consequence of habitat fragmentation is an increase of the ratio of edge to interior, because at the edges the populations are exposed to changed conditions (e.g. temperature, humidity, wind, light) partly influenced by the neighbouring habitat or association (Tscharntke et al. 2002). This environmental and biotic change associated with edges is termed edge effect (Saunders et al. 1991). Species react to edges different way; based on studying the population movements of arthropods, Duelli et al. (1990) grouped species according to their distribution around habitat borders.

In the edges of habitats the microenvironmental conditions are different from those in the interiors. This directly influences the structure of the vegetation and thereby the prevalence of animal species (Báldi and Kisbenedek 1999). In her review Murcia (1995) divided edge effects into three different types: (1) abiotic edge effects refer to changes in

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abiotic environmental factors, which are consequences of the proximity of a structurally different matrix around the habitat patch; (2) direct biological edge effects refer to the changes in abundance and distribution of species due to the direct physical proximity of edges; (3) indirect biological edge effects refer to the changes in ecological interactions among species (e.g. predation, pollination, competition, etc.). The fragmented forests, or rather the forest patches, are usually surrounded by a matrix of lower biomass and different structural complexity, e.g. pastures, cropland or secondary growth (Murcia 1995). These differences result in differences in microenvironmental factors, including temperature, humidity and light intensity on both sides of an edge (e.g. Matlack 1993; Jose et al. 1996; Báldi 1999; Urbina-Cardona et al. 2006).

From conservation point of view nature reserve should minimise the edge-to-area ratio to maximise the effective core area of the reserve (Debinski and Holt 2000). Though the species richness is generally higher in the habitat edges than in the habitat interiors (e.g. Kunin 1998), the situation can be different from this if we focus on the habitat specialist species, which have more conservation interest. For example, Magura and Kődöböcz (2007) showed an increase in total species richness of carabid beetles with decreasing habitat area in fragmented sandy grasslands, but if they analysed only the habitat specialists, they found the contrary result, i.e. specialists' richness decreased with decreasing habitat area. In case of butterflies, Krauss et al. (2003) found that the density of specialists and not that of generalists increased with increasing habitat area of calcareous grasslands.

Regarding the direct biological edge effects on butterflies we found some studies comparing edges with interiors or different types of edges at the community level (DeVries et al. 1997; Meek et al. 2002; Kitahara 2004). Another group of studies concentrated on investigating the edge effect on movement behaviour of butterflies (Schultz and Crone 2001; Schtickzelle and Baguette 2003; Ross et al. 2005; Conradt and Roper 2006). These demonstrated that the behaviour of butterflies changes significantly near edges. There are fewer studies regarding the edge effect at the population level. For example, Bergman (1999) studied the habitat utilisation of *Lopinga achine* females in open woodland and showed an edge effect on oviposition sites of butterflies, with more ovipositions at the edges of glades. The contrast in the structure of vegetation between the edge and matrix could largely determine the intensity and magnitude of edge effect. In this context Ries and Debinski (2001) investigated the response (crossing or turning back) of a habitat specialist (*Speyeria idalia*) and a generalist (*Danaus plexippus*) butterfly species to four types of prairie edges. The four edges under investigation differed in structural complexity, ranging from low-contrast to high-contrast. Based on direct

tracking they found that the specialist species avoided the edges or turned back, while only high-contrast edges affected the generalist species negatively.

Though *Maculinea* butterflies are among the insects most frequently studied (Kühn et al. 2005), there are no direct edge studies regarding these butterflies (with the exception of some studies of habitat fragmentation). In the case of *M. teleius* and *M. nausithous*, Nowicki et al. (2005a; 2007) showed that patch area negatively affected the population density in Poland, while fragmentation affected it positively. Kőrösi (2005), who only investigated the abundance of *M. teleius* adults, found that the number of individuals increased with the size of habitat patches in Hungary. Regarding *M. nausithous* there is no contradiction in the recent results. All the studies (Anton et al. 2005; Loritz and Settele 2005; Nowicki et al. 2005b) showed that the species occurred with higher frequency and in higher densities in smaller patches than in larger ones. Kőrösi (2005) indicated that this species occupied primarily the shaded areas of forest edges.

Based on the above mentioned studies we hypothesise that both study species could be affected by the proximity of edges, but *M. teleius* negatively, while *M. nausithous* positively. Further we hypothesise that meadow edges characterised by trees, i.e. hard edges would benefit *M. nausithous*, but not *M. teleius*. Therefore the aim of the present study was to test the edge effect (edge versus interior) as well as the effect of edge type on microenvironmental factors and densities of foodplants available for *M. teleius* and *M. nausithous* and consequently on local prevalence of the two butterfly species.

Methods

Study species

Both study species (*M. teleius* and *M. nausithous*) are endangered throughout Europe, and show declining population trends (Wynhoff 1998; Van Swaay and Warren 1999). Habitat loss and habitat degradation due to agriculture intensification and abandonment of traditional management threaten the species in Hungary as well. Both study species occupy wet meadows and lay their eggs in the flowerheads of their foodplant, Great Burnet (*Sanguisorba officinalis*). The species are obligatory myrmecophiles. The primary host ant species of *M. teleius* is *Myrmica scabrinodis* (though four other ant species were recorded as hosts in Hungary: *Myrmica rubra*, *Myrmica salina*, *Myrmica speciosoides* and *Myrmica gallienii*), while the only host ant species of *M. nausithous* is *M. rubra* in Hungary (Tartally and Csósz 2004; Tartally and Varga 2005). After developing on the foodplant, caterpillars are adopted by given *Myrmica*

host ants and then live in their nests as social parasites preying on ant broods (Thomas 1984; Thomas et al. 1989).

Study area

The study area was situated in the Szentgyörgyvölgyi stream valley at Velemér (Western Hungary, Őrség National Park, 46°44'N, 16°21'E, 204 m a.s.l.). The area of the valley along the stream was characterised by meadows and croplands disrupted by small paved and unpaved roads. Directly next to the stream there was a very dense alder tree strip with a height of 10–15 m. According to the traditional regime the first mowing of the year was in May and the second in late August or early September. Nowadays most of the meadows are mown once a year or every second or third year and there is no control on the timing of management during the season. None of the meadows in the valley were fertilised or treated with pesticides, and all are protected.

Field sampling

We have chosen 10 meadows (mean area = 2.5 ha) situated along a 2.5 km long section of the stream for sampling (Fig. 1). The meadows had not been mown until the end of August in the study year and had road and tree edges. We designated four 50 m long and 5 m wide transects on each meadow. One transect pair was designated at the so-called tree edge: one of the transects directly next to the trees at the stream (hereafter tree edge) and the other 15 m further inside parallel to the edge transect (hereafter tree interior). On the same meadow we used one transect pair in the same way at the so-called road edge. The road edge transect pair was situated next to a paved or unpaved road where there were no trees or bushes and only rare automobile traffic. On the other side of the road there was another meadow in all cases. One of the transects was directly at the edge (hereafter road edge), while the other was 15 m inside and



Fig. 1 Sample sites of *M. teleius* and *M. nausithous* in the Szentgyörgyvölgyi stream valley (Western Hungary, Őrség National Park). The dotted areas are wet meadows with presence of blooming foodplant of the butterfly species; the numbered meadows were selected for the study. The short parallel black-and-white dashed lines

indicate the tree edge and tree interior transects, while the short parallel black lines indicate the road edge and road interior transects. The space photo was provided by the Fertő-Hanság & Őrség National Park Directorate

parallel to the previous one (hereafter road interior). The two interior transects on the same meadow were as far as possible from each other. We detected the number of *M. teleius* and *M. nausithous* individuals at each transect, walking along the transects in 2 min once everyday during the peak of flight period from the 24th to the 31st of July in 2006, eight times altogether. Within the 5 m wide transects the detectability of the two species was assumed to be constant. We paid attention not to count any individual more than once during each transect sampling. We carried out butterfly observations on sunny days without strong winds, from 9:00 a.m. until 4:00 p.m. After the 31st of July no more sampling was possible because of a long period of cold and rainy weather. To obtain unbiased data, the order in which meadows were sampled was varied between days. In the case of *M. nausithous* three meadows in which fewer than six individuals (probably transient animals) were observed during the study were excluded from the analysis. During every transect count we measured the temperature and the relative humidity using an electronic multi-purpose thermo-hygrometer (TFA 30.5007). We held the instrument in our shadow for 2 min. Wind speed was measured using Kaindl Windmaster 2 holding the instrument for 2 min above our head. We counted the blooming shoots of foodplant once on each transect in a 1 m wide strip. We did not investigate the flora of the study area, because on the basis of our earlier direct tracking study we had found that these butterflies rarely alight to feed on the nectar of plants different from the foodplant (Kőrösi et al. unpubl.).

Statistical analysis

We used linear mixed models to test the effect of edge type (tree versus road) and edge effect (edge transect vs. interior transect) on the number of butterflies detected per transect, the microenvironmental variables (temperature, humidity and wind speed) and the foodplant of the butterflies. We decided to analyse microenvironmental variables and foodplant in separate models (i.e. we did not include these variables in the models of the butterflies), since those were highly intercorrelated with edge type and distance from edge and also partly with each other. Before the analyses species densities were pooled over sampling days, while the microenvironmental variables were averaged for the whole sampling period. We assessed the normality of the distribution of the raw dependent variables using normal quantile plots. The three microenvironmental data proved to be normally distributed, while species densities and foodplant shoot density did not follow a normal distribution. In these cases we analysed the data using log-linear models employing the Poisson distribution (Faraway 2006). In all models we included effect of edge type (tree versus road) and edge effect (edge transect versus interior

transect) and their interaction as fixed factors, but we discarded non-significant interactions ($P > 0.05$) using a manual stepwise backward selection procedure. Further, all models contained meadow as a random factor. We tested the significance of the fixed effects using the *F*-test. Conducting the model diagnostics, we always checked if the residuals of the models were normally distributed. To analyse the relationship between the butterflies' density and microenvironmental factors and foodplant, we performed Spearman rank correlations. We performed all statistical analyses using R software packages (version 2.2.0, R Development Core Team 2005).

Results

Altogether we registered 879 individuals of *M. teleius* and 92 individuals of *M. nausithous* during the study period. Analysing the effect of edge type (tree versus road) and edge effect (edge transect versus interior transect) on the density of *M. teleius*, we found a strong edge type effect, with more butterflies in road transects than in the tree transects (Table 1, Fig. 2). Although we did not show edge effect, the density was a bit higher at the road edges than at the road interiors. In the case of *M. nausithous* we found an edge effect on the density of butterflies, with higher densities at the edges (Table 1, Fig. 2). Furthermore, we showed a strongly significant edge type effect on the density of *M. nausithous*, i.e. we found the species more

Table 1 Linear mixed models for testing the effects of edge type (tree versus road) and distance from edge (edge transect versus interior transect) on the abundance of Scarce Large Blue (*M. teleius*) and Dusky Large Blue (*M. nausithous*), on three microenvironmental variables (temperature, humidity and wind speed) and on the foodplant (*S. officinalis*) of the butterflies

	Factor	<i>F</i>	<i>P</i>
<i>Maculinea teleius</i>	Edge type	26.016	<0.001
	Distance	1.032	0.319
<i>Maculinea nausithous</i>	Edge type	11.411	0.002
	Distance	19.923	<0.001
Temperature	Edge type	2.846	0.103
	Distance	2.305	0.140
Humidity	Edge type	2.090	0.160
	Distance	9.181	0.005
Wind speed	Edge type × distance	8.020	0.009
	Edge type	44.174	<0.001
	Distance	9.462	0.005
	Edge type × distance	5.579	0.026
Foodplant	Edge type	31.414	<0.001
	Distance	13.494	0.001

Bold *P* values indicate significant effects

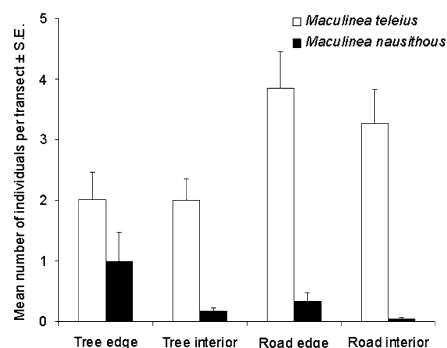


Fig. 2 Bars indicate means with SE of number of Scarce Large Blue (*M. teleius*) and Dusky Large Blue (*M. nausithous*) per transect count on two types of edges and interiors of meadows measured along 40 transects

prevalent at the tree transects—especially at the tree edge—than at the road edges (Fig. 2).

Regarding the microenvironmental parameters, we did not show either edge effect or edge type effect on air temperature (Tables 1, 2). In the case of relative humidity we found, in addition to a significant edge effect, a significant edge type—distance from edge interaction, which means that the edges were more humid than the interiors at the tree edges (Tables 1, 2). Finally, in the case of wind speed, we found both effects (edge effect and edge type effect) and a significant interaction. The tree edge was less windy than the tree interior. However, there was no similar difference between the road edge and road interior, which is the reason for the interaction (Tables 1, 2). Both the edge type and the distance from edge affected the foodplant density. The highest density was at the road interior and the lowest was at the tree edge (Tables 1, 2, Fig. 3).

Performing Spearman rank correlations between total density of *M. teleius* and foodplant shoot density and microenvironmental factors, we found that butterfly density correlated significantly negatively with air humidity ($r_s = -0.41$, $P = 0.009$) and significantly positively with foodplant shoot density ($r_s = 0.52$, $P < 0.001$). In case of

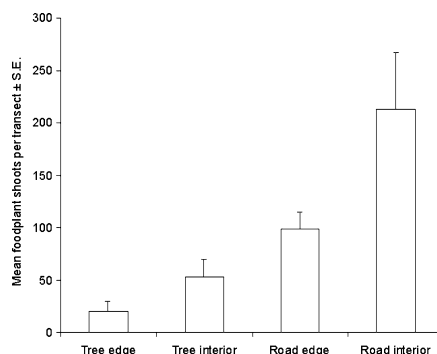


Fig. 3 Mean ($\pm$ SE) foodplant (*S. officinalis*) shoot density on two types of edges and interiors of meadows

M. nausithous we found a significantly negative relationship between butterfly density and wind speed ($r_s = -0.53$, $P < 0.001$) and also a significantly negative relationship between butterfly density and foodplant shoot density ($r_s = -0.40$, $P = 0.010$).

Discussion

In general we registered *M. teleius* in relatively high density. The species favoured the road edge and interior, while the rarer species, *M. nausithous* occurred more frequently at the edges of meadows, especially at the tree edge. So both hypotheses of the current study were supported by the results. In contrast to the distribution of butterflies, the behavioural responses of some species are well documented, e.g. Schultz and Crone (2001) found that a prairie lycaenid species (*Icaricia icarioides fenderi*) modified its behaviour within 10–22 m of the habitat boundary. Kuefler and Haddad (2006) showed different responses of four North-American Satyrinae butterfly species to boundaries with different contrasts. Ide (2002) reported seasonal changes in the microdistribution of *Lette diana*. The males of the May–June and September–October generations preferred forest edges in contrast to the July–August generations, which preferred forest interiors; because of different light conditions. There are studies that reported association of butterfly species with habitat boundaries or edges, but these earlier papers described this in the case of a single species or in species that are in the same family and have different levels of habitat specialisation (Bergman 1999; Ries and Debinski 2001). In the present paper we compared two sympatric, congeneric species (*M. teleius* and *M. nausithous*), using the same foodplant (*S. officinalis*) and having a

Table 2 Mean values ($\pm$ SEM) of temperature, relative humidity and wind speed recorded in the four transect types

	Temperature ($^{\circ}$ C)	Humidity (%)	Wind speed (km h^{-1})
Tree edge	31.6 $\pm$ 0.2	45.2 $\pm$ 0.5	1.7 $\pm$ 0.2
Tree interior	31.8 $\pm$ 0.2	43.7 $\pm$ 0.6	2.7 $\pm$ 0.3
Road edge	31.6 $\pm$ 0.2	44.1 $\pm$ 0.4	3.3 $\pm$ 0.2
Road interior	31.6 $\pm$ 0.2	44.1 $\pm$ 0.5	3.4 $\pm$ 0.2

similar myrmecophilous strategy, and found that these species use different niches within the same habitat.

In the case of *M. teleius* we found a negative relationship between butterfly density and humidity and a positive relationship with foodplant shoot density. In our earlier study at Kunpeszér (Kiskunság National Park, Central Hungary) we showed a positive correlation between *M. teleius* density and foodplant density (Batáry et al. 2007). In contrast to our results, Nowicki et al. (2005a, 2007) found that foodplant density does not limit either the density of *M. teleius* or the density of *M. nausithous* at metapopulation level. Regarding *M. nausithous* we showed a negative relationship with foodplant shoot density and wind speed. Based on these results we can conclude that foodplant density does not seem to limit the distribution of *M. nausithous*. This supports the results of Anton et al. (2008), who found no correlation between the density of the foodplant and *M. nausithous* abundance. Butterfly density is often related to the abundance of foodplants growing under suitable conditions rather than to the total density of foodplants (Bourn and Thomas 1993). Figurny and Woyciechowski (1998) indicated that these two species select different flowerheads of the foodplant, *M. teleius* ovipositing on younger flowerheads that are closer to the ground, shorter, and contain fewer flowers. They found that ovipositing females search for sites visually according to the phenological stage of the flowerheads of the foodplant. Perhaps the developmental stage of the flowerheads could be different depending on the transect type of the present study due to the different microclimate. Further, Thomas and Elmes (2001) showed that the different developmental stages and sizes of foodplant flowerheads also separate the places where the two species oviposit.

In short, the observed different edge type effect on the *Maculinea* species (niche segregation) could be attributed to the pattern of microenvironmental factors, foodplant density and phenology, and further probably to other factors not yet investigated, such as edge effect on host ant presence (Dauber and Wolters 2004). The detailed explanation of this pattern could be the following. On the two edges we found different microclimate conditions (the tree edge was more humid and less windy than the road edge). These conditions directly determine the distribution of the butterflies and the density of their foodplant too. Consequently the negative correlation between the foodplant and *M. nausithous* is probably the result of the microclimatic conditions, as is the positive correlation between the foodplant and *M. teleius*. The butterfly species *M. teleius* and the foodplant Great Burnet have the same microclimatic requirements. Furthermore, *M. rubra*, the host ant of *M. nausithous*, favours the wetter meadow areas and is therefore probably the dominant ant species there (Dauber and Wolter 2004; Glinka and Settele 2005), while in the interiors of the meadows and

in closer parts of road edges there could be a more diverse ant assemblage dominated by *M. scabrinodis*, which is the primary host ant of *M. teleius*. Presumably the two *Maculinea* species diverged so that in *M. nausithous* there could have been a shift in host ant species to the direction of *M. rubra*, which resulted in a preference of imagoes to a wetter microclimate (Elmes et al. 1998; Als et al. 2004). Finally the foodplant–host ant coincidence is a key question in the survival of these species. In the case of predacious species, such as *M. teleius*, the overlap is thought to be minimum 50%, whereas the coincidence of foodplant and host ant of *M. nausithous* is much lower (Thomas and Elmes 1998; Thomas et al. 1998). *M. teleius* achieves this level of co-occurrence by using several host ant species, while *M. nausithous* is highly specialized on an ant species that has a supercolony (*M. rubra*) (Elmes et al. 1998; Tartally and Varga 2005). The latter butterfly species may represent an evolutionary transition between the two strategy types, i.e. the predatory and cuckoo feeding strategies (Thomas 1991; Thomas and Settele 2004).

We investigated how different types of edges, which are generally thought to have negative effects from conservation point of view, do affect these highly specialised butterfly species. The conclusion for conservation is that interiors of meadows that are quite far from the tree edges are important for *M. teleius*, while tree edges at landscape scale level maintain the habitats of the rarer butterfly *M. nausithous* in this region. However, we did not investigate the effect of grassland management. The timing and intensity of management could also be critical in the survival of these species (Johst et al. 2006). Future studies should also focus on the relationship with host ants, as the presence of species might be a direct result of eclosion in the areas and as it might also have been influenced by previous mowing events.

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Study II

II

**Different population structure and habitat use of two
sympatric *Maculinea* butterflies at small spatial scale**

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Peregovits

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1 **Different population structure and habitat use of two sympatric *Maculinea* butterflies at**
2 **small spatial scale**

3
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19 Running title: Population structure of two *Maculinea* butterflies

20

20 **Abstract**

21 Metapopulation theory has been a major paradigm in the conservation of butterflies over the
22 last decades. Recently, several studies revealed that quality of habitat patches may have a
23 greater influence on the persistence of butterfly populations than patch size and isolation. The
24 highly specialized *Maculinea* species usually do not form classic metapopulations, but are
25 rather characterized by low population turnover and mobility. Local population processes are
26 therefore suspected to play an accentuated role in their survival at the landscape scale.
27 *Maculinea nausithous* and *M. teleius* use the same larval food plant and usually occupy the
28 same habitats in Europe, but no significant quantitative differences in the habitat use of adult
29 butterflies have been demonstrated. We aimed to test the effects of the proximity of forest
30 edges on the microdistribution and movement of the two species based on an intensive mark–
31 release–recapture sampling within one habitat fragment. Distribution of *M. nausithous* was
32 aggregated and highly positively influenced by the proportion of afforested meadow edges,
33 while *M. teleius* showed no preference for afforested edges. Movement of *M. teleius* was
34 hindered by forest strips. In both species, the vast majority of moves was restricted to smaller
35 parts of the habitat. Our results suggest that *M. nausithous* has a narrower niche in the study
36 region, which is most likely due to that its only host ant can find suitable microclimatic
37 conditions at the afforested edges of marshy meadows. This implies that different habitat
38 management is desirable for the conservation of the two species.

39

40 Keywords: forest edges, habitat management, *Maculinea nausithous*, *Maculinea teleius*,
41 myrmecophily, niche overlap.

42

42 **Introduction**

43 Butterflies are frequently used model species in population ecology, especially in studies on
44 the dynamics and spatial structure of metapopulations (see Thomas and Hanski 1997; Ehrlich
45 and Hanski 2004 and references therein). Most interest has been attracted by dispersal among
46 habitat patches, extinction-colonization dynamics and patch-occupancy patterns on landscape
47 scale (e.g. Hanski et al. 2000; Wilson and Thomas 2002; Baguette and Schtickzelle 2006).
48 Although several authors have stressed the importance of habitat use and movement patterns
49 within single habitat patches (e.g. Mallet 1986; Lindenmayer et al. 2003; Barton and Bach
50 2005), they have received relatively little attention (but see Jeanson et al. 2003).

51 Metapopulation theory has been also a major paradigm to establish ecological networks
52 (Fahrig 2001), with a special emphasis on habitat patch area and isolation in the early
53 metapopulation works. Nowadays, there is an ample evidence that habitat patch quality
54 should be explicitly considered as well (Thomas et al. 2001; McIntire et al. 2007), especially
55 for insects, as their long-term persistence may be determined by habitat quality rather than by
56 habitat configuration (Dennis and Eales 1999; Fleishman et al. 2001). This implies, that
57 conservation efforts have to be concentrated on the maintainance of high quality habitat
58 patches, which can be difficult because of the co-occurrence of several target species. In such
59 cases, the identification of ecological resources and conditions for each species is essential, as
60 well as the testing of transferability of ecological profiles between species sharing the same
61 biotope and host plant. Only detailed studies can reveal important differences in the resource
62 use of such species, which have far-reaching consequences for their conservation (Turlure et
63 al. 2009).

64 Large blue butterflies of the genus *Maculinea* have been the focus of several ecological
65 studies (Settele et al. 2005). They are obligate social parasites of *Myrmica* ants and they
66 sequentially use food plants and host ants during their larval period, providing an appropriate

67 model system for evolutionary (Als et al. 2004; Nash et al. 2008) as well as community
68 ecological investigations (e.g. Clarke et al. 1997). Moreover, *Maculinea* species are among
69 the most endangered butterflies (van Swaay and Warren 1999) and have become flagship
70 species for nature conservation in Europe (Thomas and Settele 2004). Population ecological
71 studies revealed that *Maculinea* butterflies do not tend to exist in classic metapopulations
72 (Nowicki et al. 2007), because populations are typically small, but remarkably
73 demographically stable (Thomas et al. 1998) and mobility between habitat patches is quite
74 low compared to other butterflies (Nowicki et al. 2005). Both features reduce the turnover of
75 local populations and increase the importance of their dynamics. Nevertheless, few field
76 studies have attempted to explore the habitat use and movement of *Maculinea* butterflies
77 within local populations (but see Hovestadt and Nowicki 2008; Kőrösi et al. 2008).

78 The closely related *Maculinea nausithous* and *M. teleius* often co-occur on marshy
79 meadows in Hungary and caterpillars of both species feed exclusively on the seeds of the
80 great burnet (*Sanguisorba officinalis*). Furthermore, the phenology of the two species in
81 Hungary is very similar as their flight period nearly completely overlaps. Landscape-scale
82 studies indicate that *M. nausithous* shows a preference for afforested edges of meadows and
83 abandoned grasslands, while *M. teleius* is usually more abundant in the interior parts of
84 meadows and prefers open, regularly mown grasslands (Batáry et al. 2009; Kőrösi et al.
85 *submitted*). These differences in their habitat use have serious implications for the
86 management of habitat patches where they co-occur. In the present study, we test the effects
87 of one particular ecological condition (proportion of afforested meadow edges) on the
88 microdistribution of *M. nausithous* and *M. teleius* within the same habitat fragment. Our aim
89 was to reveal whether the microdistribution of the two species is significantly different on the
90 spatial scale of a local population and to draw conclusions how these differences may affect
91 the successful conservational management of their habitats.

92

93 **Materials and methods**

94 *Study site*

95 The study area was located in the valley of the Kerca stream in the Órség National Park (W
96 Hungary, 46°46' N; 16°18' E; 240 m a.s.l.). Our study site was a piece of a marshy meadow
97 in a mosaic landscape. Approximately half of the study site had been abandoned since 1995,
98 while the other half had been mown erratically and seemed unsuitable for the butterflies in the
99 sampling period and therefore was not sampled (Fig. 1). In the abandoned part of the
100 meadow, apart from a few patches of sedges (*Carex* spp.), willow shrubs (*Salix* spp.) and
101 invasive weeds (*Solidago* spp.), the common food plant (*Sanguisorba officinalis*) of the two
102 study species was growing at high densities in distinct patches providing suitable habitat for
103 both butterflies. We designated 22 spatial units for sampling in these parts of the meadow
104 (Fig. 1). Designation of sampling units was arbitrarily adjusted to some landmarks (e.g.
105 bushes); size and shape of the 22 sampling units were variable (300–2200 m²). The sampling
106 area was surrounded by mixed deciduous forests (Fig. 1). Both *Maculinea* populations
107 occupying the study site could be regarded as single populations. According to another study
108 in 2006, these populations are probably not isolated from others in the surrounding landscape
109 (Örvössy et al. *in prep*). Outlines of the spatial units were located using GPS (Trimble
110 GeoExplorer 3) and ArcView 3.3 was used to measure perimeters, areas and distances.

111

112 *Study species*

113 Both the dusky large blue (*Maculinea nausithous* Bergsträsser, 1779) and scarce large blue
114 (*Maculinea teleius* Bergsträsser, 1779) are obligate social parasites of *Myrmica* ants. Females
115 oviposit into the flowerheads of the great burnet (*Sanguisorba officinalis*). After a few weeks
116 of feeding on the seeds, caterpillars descend to the ground and await adoption by host ant

workers, which carry them into their nest where caterpillars predate on the ant brood (Thomas 1984). In Hungary, *Myrmica rubra* is the only known host ant of *M. nausithous*, while the primary host ant of *M. teleius* is *Myrmica scabrinodis*, although four additional ant species are also recorded as its host (*M. gallienii*, *M. rubra*, *M. salina*, *M. specioides*) (Tartally and Varga 2008). In the study area, the flight period of the two butterflies overlaps (from mid July to mid August). Both species are listed by the Annex II of the Habitats Directive, since they show declining population trends throughout Europe (Wynhoff 1998a).

Sampling method

The two sympatric populations were studied by mark–release–recapture (MRR) method. Sampling took place over two weeks in the peak time of the flight period of both butterflies (31 July – 13 August 2003) and was conducted every day between 09:00 and 17:00. Butterflies were captured by net, marked on the underside of their hindwing using fine tipped waterproof pen (Edding 140 S). Species and sex of each specimen were recorded together with the time and location (code of spatial unit) of the capture event, after which the butterflies were released. Duration of sampling in each spatial unit was proportional to its area in order to standardize the sampling effort. We endeavoured to capture all butterflies in each spatial unit. As the butterflies' food plant was superabundant throughout the study site (~20–50 flowerheads m⁻²) and did not seem to be a limiting factor for the butterfly populations, we did not sample its abundance.

Data analysis

We modelled the microdistribution and emigration rate of butterflies applying different types of generalised linear models (GLM). We used two variables to characterize the distribution of butterflies: (i) abundance was measured as the sum of the daily captures in each spatial unit

142 and (ii) density was calculated as the abundance divided by the area of the spatial unit.
143 Explanatory variables were the *area* of the spatial units, the area of a 3 m wide zone along the
144 afforested edge of the spatial units (*forest edge*), and the proportion of this zone to the area of
145 the spatial units ($forest\ proportion = forest\ edge / area$). Three-metre width of the edge zone
146 was assumed as a typical budding distance of *Myrmica* ant colonies (Hochberg et al. 1994)
147 and a distance within forest edge may significantly influence the microclimatic conditions
148 (Batáry et al. 2009). Since *forest proportion* was calculated using *area*, these variables were
149 not included together in any model.

150 We calculated the emigration rate of butterflies for each spatial unit according to Sutcliffe
151 et al. (1997): number of emigrants was divided by the sum of emigrants and residents in a
152 given unit. In this case, the above described set of explanatory variables included the density
153 of males (*male density*) and the proportion of males (*male proportion*) also, because we
154 assumed that these variables could influence the emigration rate of both sexes: high density
155 (or proportion) of males may decrease the chance of males to find mating partners, while
156 females may emigrate from spatial units of high male density to avoid harassment (Baguette
157 et al. 1998). However, when pooled data of sexes was analysed, we rather used the overall
158 density to test for density-dependence of emigration rate.

159 At first, we tested for spatial autocorrelation in the response and explanatory variables
160 using global Moran's I tests. Neighbour links were defined based on distances between the
161 centroids of spatial units in the range of 0–55 m. In this way all spatial units had at least one
162 neighbour, and being aware of limited movement of *Maculinea* butterflies within habitat
163 patches (Hovestadt and Nowicki 2008; Körösi et al. 2008) we found this distance range
164 biologically meaningful. We used row-standardised spatial weights (Bivand et al. 2009).

165 We specified two models for each response variable. In the first model, the environmental
166 explanatory variables were *area* and *forest edge*, while the second model included *forest*

167 *proportion* only. In the case of emigration rates both of these model types included *male*
168 *density* (or density of pooled sexes) and *male proportion* as well. In some cases logarithmic
169 transformation of the explanatory variables highly improved the models' fit (see Table 1. for a
170 list of all models tested). In all cases we applied generalised linear models (GLMs) with
171 Poisson error distribution using quasi-likelihood estimations, because the distribution of the
172 residuals of simple linear models were non-normal and the data were overdispersed. Model
173 selection was made by dropping out variables from the full model based on F-tests. We
174 plotted the deviance residuals against the fitted values of each model to check model fit
175 (Faraway 2006). Finally, we tested for spatial autocorrelation in the model residuals using
176 Moran's I tests (Moran 1948; Dormann et al. 2007). For both species, data of males and
177 females were analysed separately and pooled also.

178 Explorative analysis of butterflies' movement distances was also performed. We
179 considered the displacement between the first capture and the consecutive recapture of each
180 butterfly as a move. Move length was measured as the Euclidian distance between the
181 centroids of sampling units where the given individual was marked and recaptured. Moves
182 were classified into two groups by that the marking and recapture had happened in the same
183 sampling unit (*residents*) or in different ones (*emigrants*). Time length between the two
184 captures in these two groups were compared by Wilcoxon rank-sum tests. Move lengths of
185 emigrants were compared between sexes and species using the same statistics. All analyses
186 were performed using packages 'maptools' (Lewin-Koh et al. 2009), 'spdep' (Bivand et al.
187 2009) and 'faraway' (Faraway 2009) of R 2.9.1 software (R Development Core Team 2009).

188

189 **Results**

190 A total of 171 and 1085 individuals of *M. nausithous* and *M. teleius*, respectively, were
191 marked. Mean abundance of *M. nausithous* in sampling units was 13.7 (range: 1–50,

192 median=10), while that of *M. teleius* was 78.5 (range: 16–171, median=65.5). Global Moran-
 193 tests showed a significant positive spatial autocorrelation for *area* and *forest proportion* of
 194 spatial units as well as for *abundance* and *density* of *M. nausithous* (Table 2). Although the
 195 global tests could not identify the exact location of positive spatial autocorrelation, the
 196 patterns could be illustrated by maps of the sampling area on which shading indicates the
 197 value of each variable (Fig. 2). These maps show that spatial aggregation of *M. nausithous*
 198 coincides with high values of *forest proportion* and small values of *area*.

199 The area of afforested edge zone (*forest edge*) had not any significant effect on butterflies’
 200 density or abundance in any one model. In the case of *M. teleius*, *area* had a significant
 201 positive, while *forest proportion* had a significant negative effect on the abundance (Table 3).
 202 Although the use of $\log(\text{forest proportion})$ improved the model fit, three sampling units with
 203 zero *forest proportion* were omitted from these models. None of the predictors had any
 204 significant effect on the density of *M. teleius*. Contrarily, both the abundance and density of
 205 *M. nausithous* were positively affected by *forest proportion*, but models for density had much
 206 higher predictive values (Table 3). *Area* had a marginally significant effect on abundance and
 207 diagnostic plots suggested a weak model fit. However, $\log(\text{area})$ had significant negative
 208 effect on density. There were no remarkable differences between sexes in any models.

209 The emigration rate of *M. teleius* was significantly influenced by all predictors with the
 210 exception of *forest proportion* (Table 4). *Area* and *forest edge* had significant negative
 211 effects. *Density of males* also had a negative effect on both males’ and females’ emigration
 212 rate, while *male proportion* affected the emigration rates positively. For the pooled data, we
 213 also found a negative relationship between density and emigration rate. For *M. nausithous*,
 214 due to the low number of captures per sampling units the emigration rate could not be
 215 modelled.

216 We recorded 77 moves of *M. nausithous* (males: 51, females: 26) and 483 of *M. teleius*
 217 (males: 157, females: 326). The frequency of residents was neither different between species
 218 (χ^2 -test: $\chi^2=0.27$, $p=0.61$) nor between sexes of each species (χ^2 -test: *M. nausithous* $\chi^2=0.02$,
 219 $p=0.89$; χ^2 -test *M. teleius*: $\chi^2=0$, $p=0.99$), which means that males and females had the same
 220 probability to stay in a given sampling unit between two consecutive captures. We found no
 221 significant differences in the time length between two captures of residents and emigrants,
 222 indicating that move length was not time-dependent. Move lengths of females were
 223 significantly longer than those of males in case of *M. teleius* ($W=10625.5$, $p=0.014$), and
 224 marginally significantly longer in case of *M. nausithous* ($W=260$, $p=0.088$). We found no
 225 differences in the move lengths between species (Figure 3). Only two individuals of *M. teleius*
 226 took a longer move than 200 m, while the longest move taken by *M. nausithous* was 190 m.

227

228 Discussion

229 We found remarkable differences in the microdistribution of the two closely related
 230 *Maculinea* species in this study. *M. teleius* did not show any sign of a non-random spatial
 231 distribution. Its abundance was positively correlated with the area of spatial units, which is an
 232 obvious result if we assume a random (or uniform) spatial distribution. Due to the negative
 233 correlation between *area* and *forest proportion*, the abundance of *M. teleius* was negatively
 234 affected by *forest proportion*, but it can not be interpreted as this species avoided the
 235 afforested edges. The explanation is rather that *M. teleius* showed a more or less even spatial
 236 distribution in the sampling site. Note, that density of *M. teleius* could not be explained by
 237 any predictors. In contrast, the density of *M. nausithous* was significantly higher in smaller
 238 spatial units, where the proportion of afforested edge zones was higher. As the sampling units
 239 were delineated arbitrarily, the only explanation for this pattern is that *M. nausithous*
 240 preferred the afforested edges of meadows and aggregated there. These results are in

241 agreement with our findings at landscape scale, where we showed a contrasting distribution of
 242 these species across different meadow edges (Batáry et al. 2009). The novelty of the present
 243 study is that we revealed the internal structure of populations at a finer spatial scale, we made
 244 quantitative estimations on the effects of forest edges on the distribution of butterflies and
 245 explored the movement of individuals within one habitat patch. Our explanation for the
 246 observed pattern is that *Myrmica rubra*, the only host ant of *M. nausithous*, prefers humid and
 247 cool soil conditions and thus it is the predominant ant species on meadow edges near to
 248 forests, where humidity is usually higher than in meadow interiors (Elmes et al. 1998; Dauber
 249 and Wolters 2004; Batáry et al. 2009). Therefore, preference for afforested meadow edges by
 250 *M. nausithous* butterflies seems to be adaptive since here the coincidence of host ants and
 251 food plants is expected to be higher than elsewhere. *M. teleius* is abundant in meadow
 252 interiors (Batáry et al. 2009), where ant communities consist of more species, but this
 253 butterfly may be reared by several *Myrmica* species (Tartally and Varga 2008; Witek et al.
 254 2008). This low host-specificity assures sufficient food plant–host ant coincidence.
 255 Furthermore, the negative area–density relationship for *M. nausithous* corresponds with the
 256 results of Hambäck and Englund (2005), who found this relationship characteristic for
 257 butterfly metapopulations in a meta-analysis. A similar pattern was revealed at landscape
 258 level by Nowicki et al. (2007) in sympatric metapopulations of *M. nausithous* and *M. teleius*.
 259 The emigration rate of *M. teleius* was negatively affected by the area of spatial units in all
 260 cases, which means that butterflies were more prone to emigrate from smaller units. The area
 261 of afforested edge zone (*forest edge*) had also a negative effect on emigration indicating that
 262 forests may constitute barriers for the emigration of *M. teleius* butterflies. Density of
 263 butterflies affected the emigration rate negatively, which can be explained by the implicit
 264 assumption that butterfly density was positively related to habitat quality and butterflies
 265 emigrated from higher quality spatial units with a lower probability. However, as we did not

266 make any measurements on microclimate, abundance of host plant and host ants, we are
 267 unable to specify the microhabitat preferences of *M. teleius* in this study (but see Batáry et al.
 268 2007). Density of males had a negative effect on emigration rate of both sexes, but we
 269 suppose that male density is a surrogate for overall density and reflects to habitat quality,
 270 since male and female density were positively correlated (Spearman's $\rho=0.67$, $p<0.001$).
 271 More interestingly, *male proportion* had a significant positive effect on emigration rates of
 272 both males and females. High proportion of males can decrease their chance to find suitable
 273 mating partners and increases male harassment that females suffer from (Baguette et al.
 274 1998). To our best knowledge, sex-biased density-dependent movement of butterflies has
 275 been found in very few studies only, and the spatial scale of such studies was much larger
 276 than in our present one (Odendaal et al. 1989; Baguette et al. 1998).

277 The lack of time-dependence in butterflies' move lengths suggests that they did not follow
 278 the rules of a pure random walk, which is a widely used null-model for animal movement
 279 (e.g. Blackwell 1997). We found a higher mobility of females, which is a general pattern in
 280 butterfly populations (e.g. Kuussaari et al. 1996; Baguette et al. 1998). However, mean move
 281 length of both species was unexpectedly small indicating that the majority of butterflies
 282 stayed within smaller parts of the sampling site. Moreover, an extremely tiny proportion of
 283 individuals took any moves in the range of the largest distances that could have been detected
 284 (~240 m). We provide different explanations for this limited within-habitat movement of the
 285 two studied species, which has already been demonstrated by Hovestadt and Nowicki (2008).
 286 As emigration rate of *M. teleius* was negatively affected by *forest edge*, we suppose that forest
 287 strips can act as movement barriers for this species. On the other hand, limited movement of
 288 *M. nausithous* is rather a consequence of its patchy microdistribution within the sampling site.

289 Although we did not consider the entire range of ecological requirements of all life stages
 290 of *M. nausithous* and *M. teleius*, we found that one particular environmental condition, the

291 proximity of afforested edges, can explain the different microdistribution of adult butterflies
292 within their habitat patches. According to our results, *M. nausithous* may have a narrower
293 niche since it preferred the afforested meadow edges, while *M. teleius* was more evenly
294 distributed throughout the sampling site. This was reflected by the aggregated distribution and
295 much lower number of captures of *M. nausithous* (but see Dierks and Fischer 2009). As a
296 consequence, the definition and management of habitats must be different for the two species.
297 We suppose that a functional resource-based concept for habitat definition would be more
298 appropriate for these butterflies, than delineating habitat patches based on the presence of host
299 plants or according to some vegetation categories (Dennis et al. 2003, 2006). This was also
300 confirmed by Anton et al. (2008) who found that the density of *M. nausithous* was
301 predominantly determined by the density of host ants, while host plant density had no effect
302 on butterfly density.

303 In the study region wet meadows serve as good habitats for *M. teleius*, but *M. nausithous*
304 can find suitable conditions on the afforested meadow edges only, which predicts the
305 existence of smaller and more isolated populations for this species. Either natural or artificial
306 extension of forest belts, hedgerows and patches of shrubs would enlarge the area of suitable
307 habitats for *M. nausithous* (and primarily for its host ant), and would rarely increase the
308 fragmentation of *M. teleius* habitats at the same time. However, beside the establishment of
309 new habitat patches, the appropriate management of the existing ones is a crucial element of
310 the successful conservation of butterflies. For example, timing and intensity of management
311 fundamentally influence the survival of large blue butterflies (Johst et al. 2006), thus further
312 research on the effects of different mowing regimes on *Maculinea* populations are urgently
313 needed (see Grill et al. 2008; Körösi et al. *submitted*).

314 Finally, we stress that our results can not be generalised across the whole European
315 distribution range of the studied species. Several authors have already investigated the

316 structure and dynamics of sympatric populations of *M. teleius* and *M. nausithous* in Europe,
 317 but none of them reported significant quantitative differences in their habitat use (Thomas
 318 1984; Wynhoff 1998b; Nowicki et al. 2005, 2007; Dierks and Fischer 2009). Some authors
 319 found differences in the flowerhead selection for oviposition of the two species, but no
 320 discrepancy in the spatial distribution of adult butterflies was detected (Thomas 1984; Figurny
 321 and Woyciechowski 1998; Thomas and Elmes 2001). We suppose that different habitat use of
 322 *M. teleius* and *M. nausithous* in Hungary is due to that the only host ant (*Myrmica rubra*) of
 323 *M. nausithous* prefers relatively cool and humid microclimatic conditions, which can only be
 324 found at the afforested edges of meadows, but this hypothesis should be empirically tested. In
 325 summary, our present study clearly demonstrates that successful conservation strategies must
 326 be based on detailed knowledge about the ecological requirements of target populations, even
 327 in the case of species with apparently similar life cycle.

328

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336

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 488

488 Legends of figures

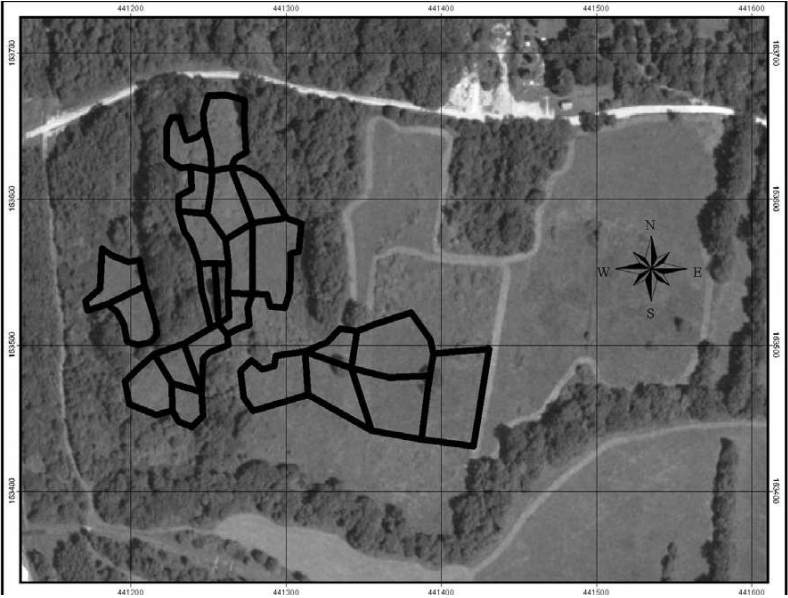
489 Figure 1. Aerial photo of the sampling area provided by the Órség NP Directorate. Thick
490 black lines delineate the 22 sampling units on the abandoned half of the meadow. Unsampld
491 eastern and northern parts of the meadow were erratically mown, while the southern part was
492 abandoned and covered by sedges. Grid cell width represents 100 m.

493 Figure 2. Maps illustrating the distribution and spatial autocorrelation of (a) *area*, (b) *forest*
494 *proportion*, (c) *abundance* of *M. teleius* and (d) *M. nausithous*. Values are classified in equal
495 intervals. Darker shading indicates higher values.

496 Figure 3. Move lengths of butterflies. Females made significantly longer moves for *M. teleius*.
497 For *M. nausithous* the difference was marginally significant.

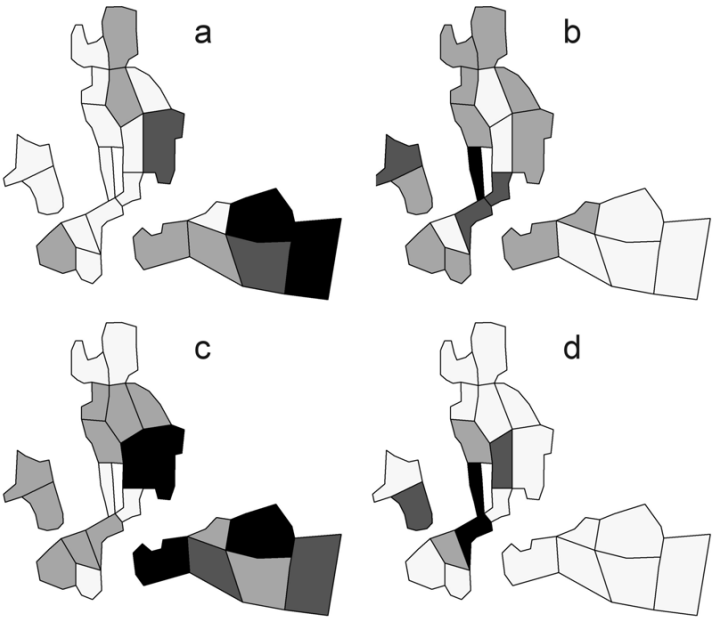
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498 Figure 1



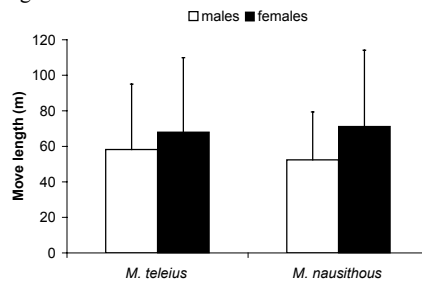
499
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502 Figure 2



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504 Figure 3



505

506 Table 1. List of generalized linear models specified and tested for both sexes of the two study
 507 species.
 508

Species	Response variable	Explanatory variables
<i>M. teleius</i>	Abundance	area, forest edge
	Abundance	forest proportion
	Abundance	log(forest proportion)
	Density	area, forest edge
	Density	forest proportion
	Emigration rate	area, forest edge, male density, male proportion
<i>M. nausithous</i>	Emigration rate	forest proportion, male density, male proportion
	Abundance	area, forest edge
	Abundance	forest proportion
	Density	area, forest edge
	Density	log(area), forest edge
	Density	forest proportion

509
 510

510 Table 2. Results of global Moran tests for spatial autocorrelation.

511

Variable	Moran's I	p-value
Area	0.392	< 0.001
Forest edge	0.031	0.28
Forest proportion	0.25	< 0.05
<i>M. teleius</i> abundance	0.08	0.17
<i>M. teleius</i> density	-0.12	0.72
<i>M. nausithous</i> abundance	0.23	< 0.05
<i>M. nausithous</i> density	0.23	< 0.05

512

513

513 Table 3. GLM results on the abundance and density of butterflies. Each row represents a
514 different model. Predictive power indicates the proportion of variance explained by the
515 model.
516

Species	Sex	Response	Predictors	Estimation (SE)	p-value	model's
						predictive power
<i>M. teleius</i>	males	Abundance	Area	0.0007 (0.0002)	0.004	0.54
			Forest_prop	-2.59 (1.05)	0.022	0.26
			log(Forest_prop)	-0.78 (0.23)	0.003	0.41
	females	Abundance	Area	0.0006 (0.0002)	0.003	0.35
			Forest_prop	-2.56 (0.82)	0.005	0.36
			log(Forest_prop)	-0.64 (0.20)	0.004	0.39
	both	Abundance	Area	0.0006 (0.0002)	0.002	0.38
			Forest_prop	-2.57 (0.83)	0.006	0.35
			log(Forest_prop)	-0.69 (0.19)	0.002	0.43
<i>M. nausithous</i>	males	Abundance	Area	-0.0009 (0.0004)	0.043	0.23
			Forest_prop	2.5 (1.1)	0.033	0.23
	females	Abundance	Area	-0.0005 (0.0004)	0.278	0.06
			Forest_prop	2.2 (1.22)	0.088	0.13
	both	Abundance	Area	-0.0007 (0.0004)	0.089	0.17
			Forest_prop	2.39 (1.09)	0.041	0.21
	males	Density	log(Area)	-1.81 (0.36)	<< 0.001	0.6
			Forest_prop	4.20 (1.18)	0.002	0.43
	females	Density	log(Area)	-1.51 (0.41)	0.002	0.41
			Forest_prop	4.06 (1.27)	0.005	0.34
	both	Density	log(Area)	-1.69 (0.37)	<< 0.001	0.56
			Forest_prop	4.15 (1.18)	0.002	0.42

517
518

518 Table 4. GLM results on the emigration rate of *M. teleius*. Male proportion had only
 519 marginally significant positive effect on the emigration rate of males, otherwise all predictors
 520 significantly affected the emigration rate.

Species	Sex	Predictors	Estimation (SE)	p-value	model's predictive power
<i>M. teleius</i>	males	Area	-0.0003 (0.00007)	< 0.001	0.58
		Forest	-0.001 (0.0004)	0.025	
		Male density	-7.62 (2.76)	0.013	
		Male proportion	0.98 (0.54)	0.086	
	females	Area	-0.0002 (0.00005)	< 0.001	0.71
		Forest	-0.0009 (0.0003)	0.006	
		Male density	-9.71 (1.97)	< 0.001	
		Male proportion	1.62 (0.38)	< 0.001	
	both	Area	-0.0002 (0.00004)	<< 0.001	0.8
		Forest	-0.0009 (0.0002)	< 0.001	
		Density	-2.80 (0.47)	<< 0.001	
		Male proportion	0.77 (0.24)	0.005	

Study III

III

Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies

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Peregovits (2008)

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Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies

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Abstract The movement of butterflies within habitat patches is usually assumed to be random, although few studies have shown this unambiguously. In the case of the highly specialized genus *Maculinea*, two contradictory hypotheses exist to explain the movement and distribution of imagos within patches: (1) due to the high spatial variance of survival rates among caterpillars, the “risk-spreading” hypothesis predicts that females will tend to make linear flight paths in order to maximize their net displacement and scatter the eggs as widely as possible; and (2) recent mark–release–recapture (MRR) data suggest that within-habitat displacement of some *Maculinea* species is constrained and that adults may establish home ranges. We tested both hypothesis by analysing the movement pattern of individuals. We also investigated whether egg laying is time constrained, which would enhance the trade-off between flying and egg laying. Thirty females of *Maculinea rebeli* (Lepidoptera: Lycaenidae) were tracked within a single population in Central Hungary. Their egg-laying behaviour and individual patterns of movement were recorded, and the latter were compared

with random walk model predictions. The population was also sampled by MRR to estimate survival rates, and four non-mated, freshly eclosed females were dissected to assess their potential egg load. Net squared displacement of females was significantly lower than predicted by the random walk model and declined continuously after the 15th move. The ratio of net displacement and cumulative move length decreased with the number of moves, supporting the hypothesis that *Maculinea* butterflies establish home ranges. We found that low survival and a low rate of egg laying prevented females from laying their potential number of eggs within their lifespan. Time limitation increased the cost of movement, providing another possible explanation for the restricted movement of females.

Keywords Home range · Myrmecophily · Oviposition · Random walk model · Risk spreading

Introduction

The specialized interactions between *Maculinea* (Lycaenidae: Lepidoptera) butterflies and other species have been under studied at length [for a review see Thomas et al. (1998a, b)]. Less attention has been paid to the behaviour of the imagos, even though an understanding of a threatened species’ mechanisms and patterns of behaviour may greatly assist in the development of conservation strategies for it (Sutherland 1998; Caro 1999).

Uniquely among European butterflies, *Maculinea* species are obligate social parasites of *Myrmica* ant colonies. All *Maculinea* species are also endangered at national or continental scales in Europe, and are consequently regarded as “flagship” species of nature conservation (Thomas and Settele 2004; Settele et al. 2005). The life cycle of

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Maculinea rebeli and its interactions with associated species have been thoroughly studied both empirically (Elmes et al. 1991a, b, 1996; Thomas et al. 1991, 1993, 1997) and in theory (Hochberg et al. 1992, 1994; Clarke et al. 1997, 1998). *M. rebeli* females lay eggs on specific host plants (typically *Gentiana cruciata*), where its caterpillars briefly feed on flowers and seed. Fourth instar caterpillars descend to the ground and await discovery by foraging *Myrmica* workers, which adopt them into their nests (Elmes et al. 1991a, b). Caterpillars do not seek host ant nests actively, and die if they hatch on a plant that is beyond the foraging range of a host ant colony (Thomas 1995; Thomas et al. 1997). Lack of adoption or adoption by non-host ants is a major cause of mortality (Elmes et al. 1991a, b). So far, studies based on counting the eggs on host plants have shown that oviposition is independent of the presence of host ants (Thomas et al. 1989; Elmes et al. 1996; Thomas and Elmes 2001; Thomas 2002; Musche et al. 2006), although Van Dyck et al. (2000) found some association between the density of *Maculinea alcon* eggs on *Gentiana pneumonanthe* and the presence of its presumed host ant species.

Due partly to apparent competition between its sequential hosts (Thomas et al. 1997), *M. rebeli* usually occupies sites where only a small proportion (<30%) of *G. cruciata* plants coincide with host *Myrmica* colonies (Elmes et al. 1996). Assuming that *Maculinea* butterflies are unable to detect the presence of host ants beneath the host plants (Thomas and Elmes 2001), and that the distribution of *Myrmica* colonies is primarily affected by microclimatic conditions, the spatial variance of larval survival is inevitably high (Thomas et al. 1998a, b). Root and Kareiva (1984) suggested that in such cases “risk spreading” is a reasonable oviposition strategy. It assumes that females scatter their eggs over a wide area in order to minimize the generation-to-generation variance in reproduction rates. This hypothesis predicts that females follow linear flight paths during egg laying, eggs are usually laid singly on plants, and females pass over many suitable hosts. However, recent analyses of mark–release–recapture (MRR) data suggest that *Maculinea teleius* and *Maculinea nausithous* may establish home ranges, since their within-habitat displacement appears to be limited (Hovestadt 2005; Hovestadt and Nowicki 2005).

Animal movement can be classified by its behavioural background into routine and special movements (Van Dyck and Baguette 2005). Routine movements are associated with daily activities, while special movements involve large net displacement. In fragmented landscapes, dispersal is a by-product of special movements that are directed and cover large distances in a given unit of time (Van Dyck and Baguette 2005). Since dispersal is a key process in spatially structured populations (Hanski 1999), several studies have

investigated the behavioural aspects of dispersal in butterflies by tracking individuals (e.g. movement at habitat boundaries, Schultz 1998; Ries and Debinski 2001; Schultz and Crone 2001; Conradt and Roper 2006; foraging in the matrix, Conradt et al. 2000, 2001; or changes in movement behaviour within and outside habitat, Schtickzelle et al. 2007). Alternatively, explorative routine movements are performed within habitat patches with high levels of return and rarely contribute to dispersal in fragmented landscapes (Van Dyck and Baguette 2005). However, movement data collected within habitat patches may uncover important information about the animals’ behaviour (Mallet 1986) and studies of individual movement patterns play a significant role in the conservation of species (Caro 1999). Recently Lindenmayer et al. (2003) have stressed the importance of accurate knowledge of movement rules for the validity of population viability analyses. Metapopulation models usually assume that movement within habitat patches follows a random walk (Ovaskainen 2004; Ovaskainen and Hanski 2004), an assumption also underlying other studies (Odendaal et al. 1989; Turchin 1991; Schultz and Crone 2001). Nevertheless, the appropriateness of a random walk model for within-habitat movement of butterflies has been established in only a few cases (Kareiva and Shigesada 1983; Root and Kareiva 1984; Schtickzelle et al. 2007), while Fownes and Roland (2002) demonstrated its inadequacy.

We aimed to test the appropriateness of the random walk model for the movement of egg-laying *M. rebeli* females by analysing the flight paths of individuals. Movement patterns may differ from a random walk in two ways. The “risk-spreading” hypothesis predicts that egg-laying females follow linear flight paths, resulting in larger net displacement than predicted by random walks. Alternatively, if butterflies establish home ranges and restrict their movements to subsets of the habitat patch, net displacement will be shorter than predicted by the random walk.

We attempted to ascertain whether egg laying is time constrained or egg constrained in *M. rebeli* by estimating the egg-laying rate of females, their individual survival rates, and the potential number of eggs that an average female could produce.

Materials and methods

Study species

The taxonomic status of *Maculinea rebeli* (Hirschke 1904) is unclear, because recent cladistic studies based on either genetic (Als et al. 2004; Bereczki et al. 2005) or morphometric (Pech et al. 2004) data showed that it may only be a

distinct ecological form of *Maculinea alcon* (Denis et Schiffmüller, 1775). However, *M. rebeli* has previously been treated as a distinct species in many papers (see Elmes et al. 1991a, b; Thomas et al. 1991, 1993), so we use the term *M. rebeli* to denote the ecotype of *M. alcon*, which occupies dry calcareous grasslands in Hungary, flies from mid June to mid July and uses the cross-leaved gentian *Gentiana cruciata* (L.) as the main larval food-plant. Larvae in the population under examination feed exclusively on *G. cruciata* and are hosted by both *Myrmica sabuleti* (Mein.) and *M. schencki* (Em.) (L. Peregovits et al., unpublished data). *M. rebeli* lays single eggs on leaves and buds of the gentians. Caterpillars in the ant nests are fed by workers through trophallaxis (“cuckoo” feeding) (Elmes et al. 1991a), which is considered as a more productive (Thomas and Elmes 1998) and evolutionarily advanced form of myrmecophily (Thomas et al. 1991; Fiedler 1998; Als et al. 2004).

Study site

The study area was located in the Vértes Mountains in Central Hungary (47°26'N, 18°25'E, 365 m a.s.l.). In this region *M. rebeli* occupies dry calcareous grasslands mixed with oak–hornbeam woodland scrub. The study site was a section of grassland meadow (ca. 0.8 ha) on the fringe of an oak–hornbeam forest (Fig. 1). The meadow was surrounded by pine plantation on three sides and a native oak forest on the fourth. Some oak saplings (*Quercus petraea*), hawthorn (*Crataegus* spp.) and dewberry (*Rubus* spp.) scrub were scattered throughout the meadow.

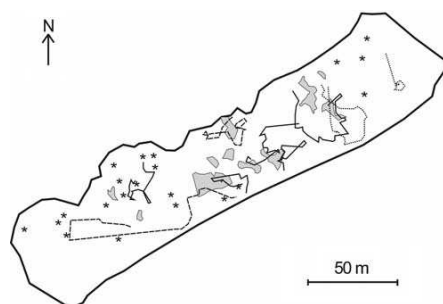


Fig. 1 Map of the study site. Asterisks indicate solitary gentian plants, grey polygons are dense gentian patches. Butterfly paths are divided into three groups: females observed to oviposit (solid lines), females observed to mate and oviposit (dashed lines) and females with no observed oviposition (dotted lines). Only nine paths out of 30 could be shown due to a high number of overlapping and/or spatially restricted (therefore not discernible) paths

Sampling method

Individual females were randomly chosen for tracking. Each female was followed until it was lost from view or stopped for >30 min. We followed at a distance of several metres to avoid influencing the butterflies' behaviour, which was recorded on a dictaphone. Each landing point was marked with a numbered flag, which corresponds to a decision being made by the butterfly, and provides more meaningful results than the use of sampling at fixed time intervals. This method also prevents problems of over- or under-sampling due to the choice of time interval between samplings (Turchin 1991, 1998). It further allowed us to observe egg-laying behaviour. At each landing point we recorded the number of gentian shoots visited and the number of eggs laid on each shoot by the female. The distance between two consecutive landing points was classed as a move, and its length and direction were measured. We intended to avoid sampling a single individual twice, but were also concerned not to affect the butterflies' behaviour, so individuals were captured and marked at the end of the tracking. The first and last landing points of each path were located by GPS (Trimble, Geo-Explorer3) and the distance between them was measured by a measuring tape to check the precision of measurement of successive moves on the path level. The deviation in the net displacement measured versus the displacement calculated from successive moves was within 1 m in all paths, indicating an acceptable degree of accuracy in our method. Sampling was carried out on 14 individual days between 20 June and 11 July 2005, between 1000 and 1700 hours under sunny and calm weather conditions.

We simultaneously carried out MRR sampling of *M. rebeli* adults to estimate the daily survival rate of the females. Butterflies were captured in nets, individually marked with fine-tipped waterproof pens (Edding 140S) on the underside of the hind wings and immediately released at the place of capture. Sampling was conducted on 14 days under suitable weather conditions. Four freshly eclosed, non-mated females were dissected and ova were counted in order to obtain a rough estimate of their potential egg load.

A map of the site was drawn using GPS to plot the positions of solitary gentian plants or the outlines of dense gentian patches (Fig. 1). Gentian shoots rather than plants were considered as the measurement unit of host plants, because shoots can always be distinguished. Thus the total number of gentian shoots was counted over the whole site.

Statistics

The flight paths of butterflies are typically circuitous, but can be approximated by a series of connected straight line

moves between the consecutive landing points (Kareiva and Shigesada 1983; Root and Kareiva 1984; Turchin et al. 1991; Turchin 1998). Quantitative analysis of path data was based on the discrete random walk approach, which allowed us to use only two simple parameters: move lengths and turning angles between successive moves. Correlated random walk (CRW) is a simple random walk formulation in which the distribution of turning angles is not uniform, inducing persistence in the direction of movement.

Net squared displacement (R_n^2) is a characteristic of paths and refers to the square of the net displacement of an individual after n moves. Comparing R_n^2 of observed paths with its theoretical distribution provides a test of the appropriateness of the CRW model. Observed R_n^2 was calculated for each n (number of moves) by averaging the net squared displacement after n moves for all observed paths that consisted of at least n moves. Since the length of observed paths varied in our data set, observed R_n^2 for low n is an average over all paths, but as n increases fewer paths are used. Theoretical values of R_n^2 were calculated using a simple formula of Kareiva and Shigesada (1983) that specifies the expected net squared displacement for each value of n , but does not provide a measure of variance around this expectation. It would have been straightforward to carry out an overall bootstrap goodness-of-fit (GOF) test for CRW, but we found the move length between paths significantly different (Table 1, test 3). Thus, instead of pooling data of all individuals, R_n^2 of the observed paths was compared with theoretical values for each path separately. For each observed path, 1,000 paths were simulated by keeping the move lengths fixed to observed values and sampling the turning angles from a uniform distribution (Schtickzelle and Baguette 2003). For each n , R_n^2 was calculated in all the 1,000 simulated paths and in the observed path as well. The 95% confidence limits for R_n^2 were estimated by the 25th and 975th percentiles of R_n^2 of the simulated paths.

The ratio of the net displacement and the cumulative length of moves (R_{NC}) is an indicator of movement directionality ranging between 0 and 1. If the path is a straight line, then $R_{NC} = 1$, and if the starting and end points of the path are identical it is 0. R_{NC} was calculated

for the subpaths at each number of moves of each path, and its relationship to the number of moves was assessed by a linear mixed effects model, in which paths formed the random factor, since subsequent R_{NC} values of a given path were not independent from one another. In the model the variance was weighted by the power function of the number of moves in order to fulfil homoscedasticity (Pinheiro and Bates 2000).

After checking the fit of MRR data to the Cormack–Jolly–Seber model by a bootstrap GOF test using program MARK 4.2. (White and Burnham 1999), a model selection based on Akaike’s information criterion (AIC) values was performed, and the parameter estimations of the most supported model were accepted.

Females usually probed the surface of the host plant with the apex of their abdomen before oviposition, a form of behaviour that we called “egg-laying investigation”. These investigations did not always result in oviposition. The number of eggs laid on each successful oviposition was recorded. The relationship between the number of eggs laid and other variables on the path level (number of moves, duration of path, sum of move lengths) was assessed using linear models.

Simulations were programmed into R code, and data management and analyses were performed using SciViews–R companion applications (R Development Core Team 2005; Grosjean and Lecoutre 2005). Some test results are presented in tables to offer an easy overview of the hypotheses tested on the data.

Results

Movement characteristics

We sampled 30 flight paths involving a total of 412 moves (from five to 24 moves per path, median number of moves = 14). The average tracking time was ~50 min. Move length followed a log-normal distribution (Table 1, test 1) and differed significantly between paths (Table 1, tests 2 and 3). No autocorrelation (order 1–5) between the consecutive move lengths of a given path was detected

Table 1 Statistical tests on move length (Zar 1999, p 591)

	Null hypothesis tested	Test name	Test statistic	<i>P</i> -value
Test 1	Log-normal distribution	Kolmogorov–Smirnov	$D = 0.0412$	0.479
Test 2	Equality of variance between paths	Bartlett (on log-transformed move length)	$\chi^2 = 29.76$	0.426
Test 3	Equality of means between paths	One-way ANOVA	$F = 2.3184$	<0.001
Test 4	No autocorrelation between length of consecutive moves	Pearson’s correlation coefficient on consecutive lengths (with lag = 1–5)	9 significant ($P < 0.05$) ρ out of 136	

Table 2 Statistical tests on turning angle (Fisher 1993)

	Null hypothesis tested	Test name	Test statistic	P-value
Test 1	Uniform vs. unimodal distribution with mean = 0	Rayleigh test for uniformity against a unimodal alternative with mean = 0	$R = 0.0381$	0.1452
Test 2	No autocorrelation between consecutive turning angles	Circular-circular (T-linear) correlation coefficient on consecutive turning angles (with lag = 1–4); P-value estimated by permutation test	6 significant ($P < 0.05$) ρ out of 105	

(Table 1, test 4): the length of a given move did not depend on the length of previous moves, so the first assumption of the CRW model was fulfilled.

The distribution of turning angles did not differ significantly from uniform (Table 2, test 1). Since the uniform distribution is symmetrical around 0, this implies that females did not show a preference for left or right turns, and more importantly that they turned in all amplitudes with the same probability. No autocorrelation (order 1–4) between the consecutive turning angles of a given path was detected (Table 2, test 2), so a given turning angle was not influenced by previous turning angles. The uniform distribution of turning angles suggests that there was no directional persistence in the movement of butterflies, so the assumption of CRW was not fulfilled. In the simpler uncorrelated random walk model the distribution of turning angles is assumed to be uniform. We therefore used its simplified formula to calculate the predicted values of net squared displacement (R_n^2).

Plotting the observed and expected values of R_n^2 against the number of moves provides a test of the fit of the random walk model. If the path is a straight line, R_n^2 increases following a parabola, which represents the upper limit of possible R_n^2 ; under the conditions of uncorrelated random walk R_n^2 grows linearly with n (number of moves), as is predicted by:

$$R_n^2 = n \times m_2,$$

where n is the number of moves and m_2 is the mean squared move length (Kareiva and Shigesada 1983). An upward curve in R_n^2 indicates a persistence in the direction of movement (correlated random walk), while a downward curve indicates some barrier to movement (Turchin 1998). R_n^2 averaged over all observed paths for each n increased linearly until $n = 15$, where it peaked ($\bar{R}_n^2 = 325.2 \text{ m}^2$, $\text{SE} = 172.30 \text{ m}^2$); after that it declined (Fig. 2). Apart from the divergence between predicted and observed values, we highlight the convex shape of the observed curve viewed from above.

When simulating 95% confidence intervals of R_n^2 for each number of moves for each path, and plotting them against the number of moves (Fig. 3), the observed R_n^2 fell below the simulated 95% confidence limit (at least for one move) in 13 out of 30 (43.3%) paths, while one path was

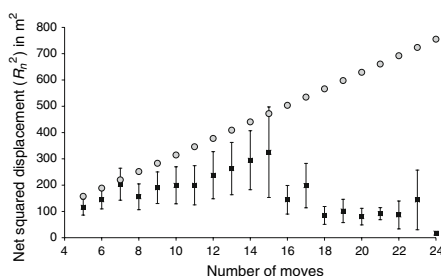


Fig. 2 Observed net squared displacement averaged over all paths (solid squares) and the predicted values of the uncorrelated random walk (grey circles) (Kareiva and Shigesada 1983) in relation to the number of moves

both above and below the confidence limits. The ten paths for which the maximum value of R_n^2 was reached at the end of the path were considered as quasi-monotonous ones. The other 20 paths were non-monotonous because the peak of R_n^2 emerged somewhere along the path (Fig. 3). Butterflies with non-monotonous paths were observed for a longer time. They made more steps but had smaller values of R_n^2 than quasi-monotonous ones (Fig. 4).

There was a significant negative relationship between the number of moves and R_{NC} values according to the linear mixed effect model ($F_{1,352} = 306.01$, $P < 0.0001$, fixed effect = -0.027 ; Fig. 5). R_{NC} equals zero when a butterfly returns to the starting point of the path predicted by the model at the ~ 22 th step. The distribution of the residuals and the random effects were normal. On Fig. 5 we fitted the fixed effect of the model to the scatterplot of the R_{NC} index and the number of moves. Since the variance of the R_{NC} index declined considerably (Fig. 5), weighting it by the power of the number of moves was appropriate in order to fulfil the homoscedasticity. The random effect explained only 5.06% of the total variance.

Egg-laying behaviour

A total of 103 investigations by 23 egg-laying females were recorded on 98 different gentian shoots. More than one egg-laying investigation was observed on five shoots,

Fig. 3 Observed net squared displacement and simulated 95% confidence intervals (CIs) for four different observed paths. *y-axis* Net squared displacement (m^2), *x-axis* number of moves. **a** Non-monotonous path, below the CI; **b** quasi-monotonous path, below and above the CI; **c** non-monotonous path, between the confidence limits; **d** quasi-monotonous path, between the confidence limits

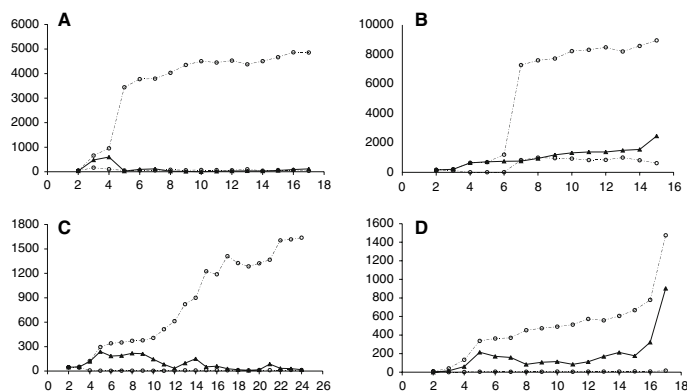


Fig. 4 A significant difference was detected between non-monotonous and quasi-monotonous paths in three variables (Wilcoxon rank sum test, $W = 48$, $P < 0.05$, $W = 27.5$, $P < 0.05$, $W = 151$, $P < 0.05$, respectively) (Zar 1999)

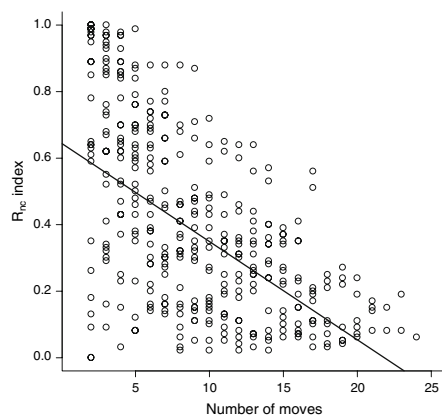
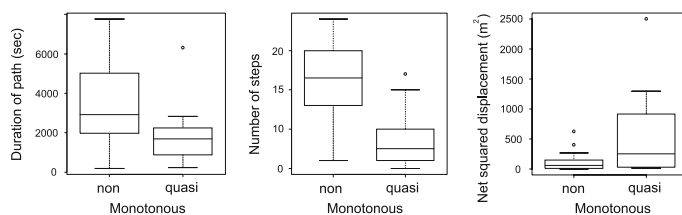


Fig. 5 The relationship between the number of moves and the ratio of the net displacement and the cumulative length of moves (R_{NC} index). The solid line indicates the fixed effect of the significant linear mixed effects model

in all cases by different females, so repeated oviposition by a female on the same shoot was never detected. Seventy-two investigations resulted in at least one egg being laid ("successful" ovipositions). Seven females did not attempt to oviposit during the observation and one individual only investigated the host plant, but did not lay any eggs. Females laid very few eggs on each occasion (for all 103 investigations, median = 2, mean = 1.92, SD = 2.21; for 72 successful ovipositions, median = 2, mean = 2.75, SD = 2.17).

We found a significant positive relationship between the duration of path and the number of eggs laid ($F_{1,28} = 5.001$, $P = 0.034$, $R^2 = 0.152$) (Fig. 6). The estimated parameter ($b = 4.763$, SE = 2.13) can be considered as an egg-laying rate (eggs/hour). R_{NC}^2 , sum of move lengths, and maximum net displacement did not show any relationship with the number of eggs laid.

In the Cormack–Jolly–Seber model with the best fit, the daily survival rate (ϕ) and the recapture probability (P) were constant over time and identical for males and females. The estimated ϕ was 0.763 (95% confidence limit lower, 0.724; upper, 0.799). The population under examination was presumably closed in terms of movement, so the

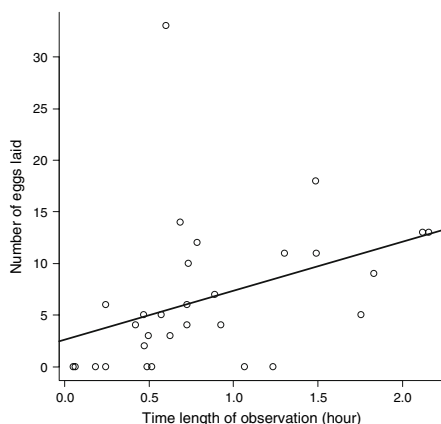


Fig. 6 Linear relationship between the duration of a path and the number of eggs laid: number of eggs = $2.57 + 4.763 \times \text{hour}$. One outlier and several females with no eggs weaken the fit of the model

average residence time (the period of time during which the population is reduced by 50%) was estimated at 2.58 days. This made it possible to estimate the total number of eggs laid per butterfly. Assuming that *M. rebeli* females are active 8 h per day, their average active lifespan is 20.6 h. Substituting this value into the equation of the linear regression of egg number and path duration, provides an estimate that an average female lays 100.9 eggs (SE = 43.9; 95% CI, 10.8–190.9). The number of ova counted in the dissected females (mean = 375.6, SD = 144.9, $n = 4$) thus greatly exceeded the estimated number of eggs laid per butterfly.

Although actual host plant distribution was not compared with theoretical distributions, we found the distribution of host plants very clumped on the sampling site: circa 82% of the gentian shoots ($\sim 1,300$ from the total of 1,585) were aggregated into a total area of 380 m² (5% of the sampling site). Thus a few gentian patches were clearly distinguished (Fig. 1).

Discussion

Our results provide a detailed description of the movements of *M. rebeli* females within a single population, including a test of the appropriateness of the random walk model. In most studies, within-habitat movement is assumed to be random (e.g. Odendaal et al. 1989; Schultz and Crone 2001; Ovaskainen 2004), but our results clearly showed that the random walk model did not describe the within-habitat

movement of *M. rebeli* females appropriately, since it overestimated the net displacement. All approaches applied in our analyses suggested that the movement of the butterflies was restricted and that they established home ranges. So far, non-random movement of butterflies has been demonstrated in the matrix and at habitat boundaries (Conradt et al. 2000; Conradt and Roper 2006), but less clearly within habitat patches. In our study, butterflies seemed to reach the boundary of their foraging range at about the 15th move, where the peak of the observed values suggested that the maximum area of the butterflies' foraging range is $325 \pm 172 \text{ m}^2$, an unexpectedly small value.

The observed value of R_n^2 was significantly smaller than predicted by the random walk model in 43.3% of the paths, indicating the inappropriateness of this model. Although the division of paths into quasi- and non-monotonous types was slightly arbitrary, the significant difference between the two in the number of moves, path duration and net squared displacement (Fig. 4) allowed us to conclude that the longer a butterfly was tracked, the more moves it made and the smaller its net displacement. This is in agreement with findings shown in Fig. 2: after the 15th move the average net squared displacement tended to decrease.

The significant negative linear relationship between the number of moves and the R_{NC} index means that the distance covered by the flight path of the butterflies increased much more slowly than the number and cumulative length of moves. At approximately the 20th move the values of R_{NC} approach zero. One possible explanation is that butterflies foraged in a restricted area, and after about 20 moves returned to the vicinity of the starting point of the path. Due to the lack of autocorrelation in the turning angles, we exclude the possibility that *M. rebeli* females had any systematic movement patterns (such as foray loops). We conclude rather that their movement was restricted primarily to the proximity of small but dense gentian patches (Fig. 1).

The females under observation never left the habitat and seldom approached its boundaries, so we rule out the possibility that frequent interferences with habitat boundaries modified their movement patterns. Furthermore, if butterflies had frequently bounced back at habitat boundaries, this would have been expressed in the distribution of turning angles, resulting in divergencies from the observed uniform distribution.

The observed movement pattern departed from that predicted by the risk-spreading hypothesis. However, the results do not disprove the other two predictions of the risk-spreading hypothesis (Root and Kareiva 1984), because *M. rebeli* females laid eggs singly and very few eggs were laid per shoot by a single female.

The estimated apparent daily survival rate is in agreement with previous studies on *Maculinea* species (Pfeifer

et al. 2000; Árnýas et al. 2005; Nowicki et al. 2005a, b). The estimated number of eggs laid per butterfly provides only a rough approximation, but it is nevertheless consistent with the results of Hochberg et al. (1992), who used a different approach. Our estimate could be imperfect if the butterflies change their egg-laying rate over time (Morales and Ellner 2002), but this is unlikely in an insect with such a short reproductive stage.

Even if our estimates of the daily survival rate and the egg-laying rate contain uncertainties, the large difference between the egg load and the estimated number of eggs actually laid by a female over its lifetime suggests that egg laying of *M. rebeli* is time constrained, which is a widespread phenomenon among butterflies (e.g. Kingsolver 1983; Doak et al. 2006).

The clumped distribution of gentians is typical of most *M. rebeli* sites (Elmes et al. 1996). Both field studies and modelling demonstrate that *Maculinea* caterpillars cause considerable damage to ant nests and reduce their competitiveness (Thomas et al. 1997). Since caterpillars depend on specific host plants for their early development, those parts of the habitat that lack gentians provide refuges for the host ants. Indeed, the long-term persistence of this butterfly on a site depends on the presence of such refuges (Elmes et al. 1996; Clarke et al. 1997; Thomas et al. 1997).

We suggest two major reasons for the restricted movement of females. First, it can be shown that even a home range of observed mean size (325 m²) can be enough for a female to avoid sibling competition, if it contains a high density of food plants. Using Hochberg et al.'s (1994) values for host ant foraging range (10 m²), Elmes et al.'s (1996) higher (30%) value for host ant incidence and Thomas and Elmes' (1998) values for the mean capacity of a *Myrmica* nest to support *M. rebeli* (5.3 pupae per nest), we can calculate that a *M. rebeli* female's mean home range contains 9.75 exploitable host ant colonies capable of rearing a total of 52 *M. rebeli* larvae to adulthood each year. Combining our values of lifetime natality (101 eggs per female) with Hochberg et al.'s (1992) values for *M. rebeli* egg and larval density-independent survival on gentians (0.758) and density-dependent larval survival on gentians, we obtain a figure of 42–54 pre-adoption larvae per female each year (see calculations in ESM). In addition, competition between siblings is further reduced due to polymorphic growth of caterpillars: 75% of the cohort take 2 years to develop per host-ant nest and 25% take 1 year (Thomas et al. 1998a, b). As described, females spread their eggs fairly evenly within their home ranges, thus even as small an area as 325 m² is sufficient to lay the maximum number of eggs in their lifetimes whilst avoiding sibling competition. However, the period of time during which our observations were made was short and we cannot be sure that females spend all of their lives within such small home

ranges. The other cause of restricted movement may be the time-constrained nature of egg laying. Time limitation increases the costs of flying, since it not only consumes energy but also time. In summary, the benefits for females of greater movement are poor due to the unpredictability of larval survival and the ease with which sibling competition can be reduced, while the costs are high: thus, restricted movement may result in a higher reproductive output per female.

Our results confirm the suggestion of Hovestadt (2005) and Hovestadt and Nowicki (2005) that *Maculinea* butterflies may establish home ranges within habitat patches. The concordance between our and their results is particularly interesting, because they employed MRR techniques, so their conclusions derive from an analysis of patterns (the spatial distribution of individuals). By tracking individuals, we gained a deeper insight into the process (movement of individuals) that generates the pattern, and we were able to combine this process with the spatial distribution of resources. It is important also to note that Hovestadt (2005) and Hovestadt and Nowicki (2005) studied populations of *M. teleius* (and *M. nausithous*), a predatory species the host plant of which (*Sanguisorba officinalis*) is abundant and evenly distributed on most of the sites.

Finally, the restricted movement of females does not allow us to infer the rate of interpatch dispersal, but only to endorse the presumption of Hovestadt (2005) that dispersal is a very rare and special event in the life of *M. rebeli* females, since the females under observation never left the habitat patch.

Both the limited within-habitat movement and the rare interpatch dispersal have implications for conservation, since they can amplify the effects of fragmentation for populations. Elmes et al. (1996) stressed that the most important factor essentially affecting the size and persistence of *M. rebeli* populations is the distribution of host plants, which was later confirmed in simulation studies (Clarke et al. 1997, 1998). Additionally, in the absence of management, suitable sites often become overgrown by scrub, making the habitat unsuitable for the butterfly (Dolek et al. 1998). We emphasize the role of linkage between gentian patches in order to decrease the spatial fragmentation of populations. The movement of butterflies between these patches should be facilitated by cutting the scrub and saplings.

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Study IV

IV

A kaszálás hatásának vizsgálata a vérfű hangyaboglárka (*Maculinea teleius*) populációira – egy kezelési kísérlet első tapasztalatai

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Természetvédelmi Közlemények (in press)

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teleius*) populációira – egy kezelési kísérlet első tapasztalatai

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Összefoglaló

A hangyákhoz kötődő, szociális parazita életmódjukról ismert hangyaboglárkák (*Maculinea spp.*) megkülönböztetett figyelemmel bírnak az európai természetvédelemben, így élőhelyeik megőrzésére hazánkban is nagy hangsúlyt kell fektetni. A nedves gyepterületeken élő vérfű hangyaboglárka élőhelykezelésének tudományos megalapozására 2007-ben egy hosszú távú kísérletbe kezdtünk az Őrségi NP területén. Az eltérő kaszálási módok hatásának vizsgálatára a Szentgyörgyvölgyi-patak mentén 4 réten jelöltünk ki 4–4 kezelési sávot, melyekben az alábbi kezeléseket folytatjuk: májusi, szeptemberi, májusi és szeptemberi kaszálás, illetve kaszálás nélküli kontroll. A kezelési sávokon belül kialakított kvadrátokban minden évben elvégezzük a tápnövény (*Sanguisorba officinalis*), a gazda hangyafajok (*Myrmica spp.*) és a hangyaboglárka imágók mennyiségének felmérését. A kaszálás hatása az egyes réteken hasonló volt, a köztük lévő cönológiai és kezeléstörténeti különbségek ellenére: az intenzívebben kaszált részeken nagyobb volt a lepkék és tápnövényük denzitása, a kevésbé kaszált területeken pedig a gazda hangyák gyakorisága volt magasabb. Ez utóbbi területek refúgiumként szolgálhatnak a hangyák számára, melyek biztosítása a hangyaboglárka fennmaradása szempontjából elsődleges, és csak mozaikos kezeléssel valósítható meg.

Kulcsszavak: biodiverzitás, gyepterkezelés, hangyagazda, kaszálás, mirmekofília, *Myrmica*, szociális parazitizmus, tápnövény

Bevezetés

Európában mára számos faj csak az elmúlt néhány ezer év során folyamatos emberi beavatkozások által alakított, változatos kultúrtájukban maradt fenn (Plieninger *et al.* 2006, Vos & Meekes 1999), ezért a különféle mezőgazdasági tevékenységek élővilágra gyakorolt hatása fontos vizsgálati eleme mind a hazai, mind pedig az európai természetvédelmi biológiának. A nyílt élőhelyek esetében a kaszálás gyakorisága, időzítése, a legelő állatok faja és mennyisége nagymértékben befolyásolhatja a vegetációszerkezetet és az állatközösségek összetételét (pl. Öckinger *et al.* 2006, Batáry *et al.* 2007). Hazánkban az Őrség területén még nagy kiterjedésű természetközeli rétek találhatók, melyek fenntartása a természetvédelem fontos feladatai közé tartozik. Mivel azonban ezek jórészt nem a Nemzeti Park kezelésében állnak, ezért olyan kezelési eljárásokat kell találnunk, melyek a gazdálkodók számára is elfogadhatók és az élőhelyek hosszú távú fennmaradását is biztosítják.

Az obligát szociális parazita életmódjukról közismert hangyaboglárkák (*Maculinea* spp.) a nagypettyes hangyaboglárka (*M. arion*) angliai kipusztulása után kerültek fokozatosan a konzervációbiológiai kutatások középpontjába (Thomas 1980) és napjainkban az európai természetvédelem „zászlóshajó” fajai közé tartoznak (Thomas 1995, Thomas & Settele 2004). E lepkefajok teljes életciklusuk során nem csupán lárvális tápnövényükre vannak utalva, hanem szükségük van a tápnövény közelében található *Myrmica* hangyafészkekre is, hiszen a hernyók fejlődése döntő részben a hangyafészkekben zajlik, ahol a fajok egy része obligát módon a hangyák lárváit fogyasztja, másik csoportjuknál pedig a hernyókat a hangya dolgozók etetik (Thomas 1995). Bonyolult életmenetük következtében a lepkéknek speciális élőhelyigényeik vannak és állományváltozásuk jól jelzi az élőhelyükön végbemenő változásokat (Munguira & Martin 1999, Thomas 1995, Wynhoff 1998). Emellett egyes vizsgálatok tanúsága szerint a *Maculinea* fajok jelenléte egy adott élőhelyen nagy biológiai sokféleséget jelez (Maes & Van Dyck 2005, Skórka *et al.* 2007, Varga *et al.* 2005).

A fentiek alapján az Őrségi Nemzeti Parkkal szoros együttműködésben azt a célt tűztük ki, hogy az Őrség területén hagyományos kaszálási típusok hatását vizsgáljuk a vérfű hangyaboglárka, tápnövénye és gazda hangya populációira nézve. Vizsgálatunkban négy különböző gyakoriságú és időzítésű kaszálási típust alakítottunk ki a mintavételi területeken, és ezekben minden évben megbecsüljük a lepkék, a vérfű és a hangyák mennyiségét. A kezelések 2007 tavaszán indultak, az itt közölt eredmények a 2008 nyarán készült mintavétel adatain alapulnak. Ezek jelenleg még nem alkalmasak konkrét kezelési tervek megalapozására, de bizonyos következtetések már most is levonhatóak.

Módszerek

A vizsgált faj

A vérfű hangyaboglárka (*Maculinea teleius* (Bergsträsser, 1779), Lepidoptera: Lycaenidae) lárvális tápnövénye az őszi vérfű (*Sanguisorba officinalis*). Az imágók július--augusztusban rajzanak, a nőtények tojásaikat a vérfű virágzatába helyezik. A kikelő hernyók 2--3 hétig a magkezdeményekkel táplálkoznak, majd az utolsó vedlést követően a talajra ereszkednek és várják, hogy *Myrmica* hangyafajok dolgozói megtalálják és a fészekbe cipeljék őket (Thomas 1984). A hernyók a hangyafészekben a hangyalárvákat fogyasztják, s itt érik el testtömeggyarapodásuk 99%-át (Thomas *et al.* 1989). A következő évben a fészekben történik a hernyók bábozódása és itt kelnek ki az imágók. Hazánkban a vérfű hangyaboglárkának a *Myrmica scabrinodis*, *M. gallienii*, *M. salina* és a *M. rubra* is lehet gazdája (Tartally & Csősz 2004, Tartally & Varga 2008), de minden populációnak van egy elsődleges gazdája, ami az adott élőhelyen a leggyakrabban előforduló *Myrmica* faj (ez hazánkban általában a *M. scabrinodis*). A faj legfontosabb élőhelyeinek a vérfűves

mocsárrétek és a kékperjés láprétek számítanak, de más növénytársulásokban is előfordul, ahol tápnövénye nagy számban van jelen. A faj szerepel a Natura 2000 II. függelékében, hazánkban fokozottan védett, állományai Európa-szerte csökkenőben vannak (Wynhoff 1998).

Mintavételi elrendezés

Velemér és Magyarszombatfa mellett a Szentgyörgyvölgyi-patak mentén négy rétet jelöltünk ki mintavételi területnek, melyek az Őrségi NP kezelésében állnak (térkép online függelékben). Minden réten kialakítottunk négy-négy kezelési sávot, melyekben az alábbi kaszálási típusokat folytatjuk: májusi kaszálás, szeptemberi kaszálás, májusi és szeptemberi kaszálás, illetve kaszálás nélküli kontroll. A különböző időpontokban végzett kaszálások a sarjmagasságot, a kaszálógép típusát és a kaszálás időtartamát tekintve egységes protokoll szerint zajlottak. A kezelési sávokat 20×20 méteres kvadrátokra osztottuk, ezeknek a közepén pedig 10×10 méteres kisebb kvadrátokat jelöltünk ki. A rétek korlátozott mérete miatt két réten kezelési sávonként 4, a másik kettőn pedig 3 kvadrátot tudunk kijelölni (összesen 56-ot). A lepkék mintavételezését a rajzási időszak csúcán jelölés-visszafogásos módszerrel végeztük standardizálva a mintavételi ráfordítást: a 20×20 méteres kvadrátokban minden nap 1 ember 5 percig végezte a mintavételt. A lepkék detektabilitását minden réten azonosnak tekintettük, bár külön tesztet nem végeztünk erre vonatkozóan. A mintavételi időszak 2008 július 16-tól július 27-ig tartott, a kedvezőtlen időjárás azonban nem tette lehetővé, hogy a lepkéket minden nap mintavételezzük. Mivel a nőtények tojásrakásra a vérfű virágfejeit használják, ezért szintén a rajzási periódusban végeztük el egy alkalommal a virágfejek számlálását a 10×10 méteres kvadrátokon belül. Olyan kvadrátok esetén, ahol a vérfű nagy denzitása lehetetlenné tette a virágfejek számlálását, először a vérfű hajtásokat számoltuk meg, majd kvadrátonként 10 db random módon kiválasztott hajtáson állapítottuk meg a

virágfejek számát, s ennek átlagát szoroztuk meg a hajtások számával. A hangyák mintavételezését szintén ugyanebben az időszakban, a 10×10 méteres kvadrátokban végeztük oly módon, hogy a *Myrmica* fajok napi aktivitásának csúcsán (reggel 6 és 8 óra között) kvadrátonként négy darab 10 cm átmérőjű, csalival ellátott műanyag lapot helyeztünk a talajra a kvadrát sarkától befelé két méterre, majd ezt követően 15--20 percen át figyeltük az ott megjelenő hangyákat és későbbi meghatározás céljából néhány példányt eltettünk belőlük alkoholba. Csalianyagnak méz és májkrém keverékét használtuk.

Adatelemzés

A lepkék esetében függő változóként az egyes kvadrátokban naponta megfogott egyedek számának összegét használtuk. A hangyáknál kidolgoztunk egy pontozásos rendszert az alábbiak szerint: ha egy adott csalin nem volt *Myrmica* – 0 pont; volt *Myrmica* és egyéb hangyafaj is – 1 pont, csak *Myrmica* volt – 2 pont. Ez a pontszám tehát minden kvadrátban egy 0 és 8 közé eső értéket vehetett fel (kvadrátonként 4 csali). Mind a négy, fentebb említett gazda hangya faj szerepelt a mintáinkban, de legnagyobb gyakorisággal a *M. scabrinodis* fordult elő.

A mintavételi területnek kijelölt négy rét között számos különbséget találtunk a mintavétel során. Ezt megerősítette egy időközben készült növényzeti alapállapot-felmérés, amely a rétek között esetenként jelentős cönológiai eltérést mutatott ki és a vegetációs szerkezeti sajátságokat nem a másfél éve folyó kezelésnek, hanem az azt megelőző, több évtizedes kezelési előtörténetnek tulajdonította (Bodonczi László, személyes közlés). Ezért, továbbá az alacsony mintaelemszám miatt a kaszálás hatását olyan lineáris kevert modellekkel elemeztük, amelyben random faktorként a rét kódja szerepelt. A három függő változóra készítettünk egy-egy modellt. Emellett a kaszálás hatását az egyes réteken külön is elemeztük (Kruskal-Wallis teszt). Ezt követően olyan lineáris kevert modellt építettünk,

amelyben függő változóként a lepkék száma, magyarázó változóként pedig a vérfű virágfejek száma és a *Myrmica*-pontszám szerepelt, random faktorként pedig a rét kódja. Azokban a modellekben, ahol a lepkék száma, illetve a virágfejek száma függő változóként szerepelt, logaritmus transzformációt alkalmaztunk, hogy a hibatag eloszlása közelítsen a normálshoz. Szintén ez utóbbi cél érdekében a *Myrmica*-pontszám modelljében a hibatag varianciáját rétenként különbözőnek állítottuk be. Elemzéseinkhez a nyílt forráskódú R 2.7.1 szoftvert használtuk (Pinheiro *et al.* 2008, R Development Core Team 2008).

Eredmények

A lepkék abundanciájára a kaszálás szignifikáns pozitív hatással volt. A májusban, illetve a májusban és szeptemberben kaszált kvadrátokban a lepkék száma némelyik réten 4–5-ször magasabb volt, mint a kontroll és a csak szeptemberben kaszált területeken (1. ábra, 1. táblázat). A vérfű virágfejek mennyiségét szintén pozitívan befolyásolta a kaszálás, itt is a májusi és a májusi--szeptemberi kaszálás volt szignifikáns pozitív hatással (1. táblázat). A kaszálás pozitív hatása a tápnövény mennyiségére különösen jól látszik a 2. rét esetében, ahol a kaszált területeken a virágfejek száma kb. 6–8-szor nagyobb volt, mint a kontroll területeken (1. ábra). A *Myrmica* hangyák mennyiségét azonban a kaszálás negatívan befolyásolta, mindhárom kaszálási típus szignifikáns negatív hatással volt a kontrollhoz képest (1. táblázat). Mindhárom fenti modellben azt találtuk, hogy a random faktor az összvariancia jelentős részét magyarázta, vagyis a rétek közötti variancia nagyobb volt, mint az egyes réteken belül a kezelések között. Ez abból fakad, hogy a vizsgált három változó mért értékei a négy rét között esetenként egy nagyságrenddel eltértek. A rétenként végzett tesztekkel a vérfű virágfejek mennyiségére csupán két, a lepkék számára és a *Myrmica*-pontszámra pedig csak egy réten

sikerült a kaszálás szignifikáns hatását kimutatnunk (2. táblázat). A Kruskal-Wallis teszt nem alkalmas annak megállapítására, hogy mely kaszálási típusok között szignifikáns az eltérés (Reiczigel *et al.* 2007), de a boxplot ábrák alapján következtethetünk a kezelés hatására (1. ábra). Ezek a tesztek csupán egy ponton mondtak (részben) ellent a modellek eredményeinek: az 1. réten a vérfű virágfejek száma a szeptemberben kaszált részekben kiemelkedően magas volt, de a kaszálatlan kontroll sávban itt is nagyon alacsony virágfejszámot kaptunk. Végezetül a vérfű virágfejek mennyisége nem volt szignifikáns hatással a fogott lepkék számára, a *Myrmica*-pontszám viszont marginálisan szignifikáns negatív hatást gyakorolt rá (1. táblázat).

Értékelés

Vizsgálatunkban a kis mintaelemszám és a rövid kezelési periódus ellenére sikerült a kaszálás szignifikáns hatását kimutatnunk. Fontos eredmény, hogy eltérő kezelési előtörténettel bíró és a vizsgált változókat tekintve jelentős mértékben különböző rétek esetén a kaszálás hatása nem volt ellentétes, legfeljebb egyes réteken nem volt kimutatható. Mindazonáltal a rétek közötti különbségek jelentős szerepet kaptak a modellekben, ezért a további vizsgálatokban és a későbbiekben kidolgozandó kezelési tervekben feltétlenül figyelembe kell venni a rétek cönológiai állapotát és kezelési előtörténetét.

Eredményeink azt mutatják, hogy a májusban, illetve a májusban és szeptemberben kaszált sávokban a vérfű hangyaboglárka és tápnövényének mennyisége nagyobb, mint a csak szeptemberben kaszált, vagy a kezeletlen részekben. A gazda hangyák előfordulása ezzel éppen ellentétes mintázatot mutatott.

Feltétlenül meg kell említeni, hogy a kaszálás szignifikáns hatását a négy rét adatainak összevonásakor sikerült kimutatnunk, a rétenként végzett tesztek azonban csak a 2. rét esetében mutattak mindhárom élőlénycsoportnál (lepke, tápnövény, hangya) szignifikáns különbséget a kezelések között. Ennek oka egyrészt az lehet, hogy a rétenként végzett teszteknel igen kis mintaelemszámmal dolgoztunk, és a kevésbé robusztus Kruskal-Wallis teszttel nem lehetett szignifikáns különbségeket kimutatni. Másrészt viszont az egyes rétek vegetációszerkezete és kezelési előtörténete nagyban eltért és előfordulhat, hogy a 2. rét vegetációja volt éppen olyan szukcessziós stádiumban, amelyben a tesztelt kezelési módok szignifikáns különbségeket okozhattak.

A három élőlénycsoport (lepke, tápnövény, hangyák) eltérő válasza a kaszálásra a következőképpen magyarázható. A májusi kaszálás nagy valószínűséggel elősegíti, hogy a lepkék rajzási időszakára a vérfű dominánssá váljon, ennek eredményeként a májusban kaszált területeken a vérfű borítása nagyobb lesz. A tápnövény relatíve magasabb denzitása vonzó a nőstények számára és feltételezhető, hogy a nőstények által lerakott tojások denzitása megnő. Mivel a gazda hangyák számára a vérfű közvetíti a parazita hernyókat, a magasabb vérfűborítás megnöveli a *Myrmica* fészkekre nehezedő nyomást, amit a *Maculinea* hernyók jelentenek és a parazitált *Myrmica* fészkek kompetitív hátrányba kerülnek más hangyafajokkal szemben (Thomas *et al.* 1997). Végeredményben a *Myrmica* fajok elhagyhatják ezeket a foltokat (drasztikusabb esetben kipusztulhatnak) és más fajok veszik át a helyüket (Elmes *et al.* 1998). A kevésbé kaszált részekben a tápnövény kisebb borítása és a lepkék alacsonyabb denzitása miatt kisebb a *Maculinea* hernyók által okozott kár a hangyafészkekben, így ezek a területek refúgiumként szolgálhatnak a *Myrmica* fajok számára. Alternatív magyarázatként az is lehetséges, hogy a *Myrmica* hangyák számára a kevésbé kaszált területeken kedvezőbbek a mikroklimatikus körülmények, melyek tekintetében a hangyák általában szűktűrűsűek (Elmes *et al.* 1998). Bármelyik magyarázat is a helytálló,

eredményeink mindenképpen felhívják a figyelmet arra, hogy a hangyaboglárkák két legfontosabb ökológiai forrására a kaszálás ellentétes hatással van, ezért a majdani kezelési stratégia kialakításában nagy hangsúlyt kell fektetni az élőhelyek mozaikosságának biztosítására.

Kiemeljük még, hogy a vizsgált hangyaboglárka fajon kívül a sötétaljú (*M. nausithous*) és a szürkés hangyaboglárka (*M. alcon*) is előfordul a mintavételi területen, de ezek a mintavétel során nagyon kis egyedszámban kerültek befogásra. A *M. nausithous* tápnövénye szintén az őszi vérfű, korábbi vizsgálataink alapján ez a faj inkább a rétek erdővel határos szegélyeit foglalja el (Batáry *et al.* 2009). A *M. alcon* állományai az Őrség ezen részén nagyon megritkultak, megfigyeléseink szerint ennek egyik oka az lehet, hogy tápnövénye, a kornistárnics (*Gentiana pneumonanthe*) szinte kizárólag a kaszálatlan, illetve nyár végén-ősz elején kaszált gyepterületeken található meg. Az ilyen területek száma és kiterjedése pedig egyre kevesebb.

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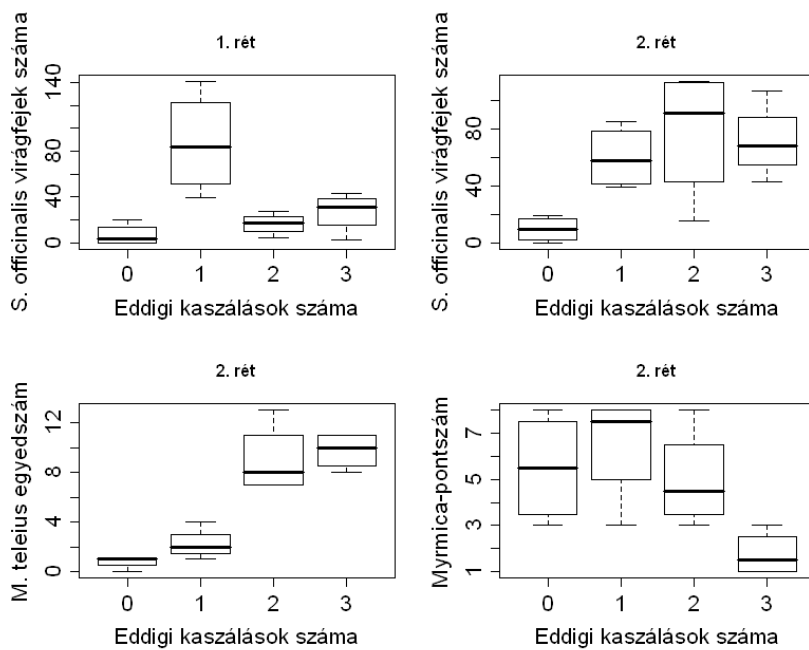
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Függő változó	Magyarázó változó és szintjei	Együttható	p-érték	random hatás
log(lepkeszám)	kaszálás szeptemberben	-0,040	0,615	57,45%
	kaszálás májusban	0,308	< 0,001	
	kaszálás májusban és szeptemberben	0,325	< 0,001	
log(virágfejek száma)	kaszálás szeptemberben	0,155	0,570	55,75%
	kaszálás májusban	0,550	0,048	
	kaszálás májusban és szeptemberben	0,616	0,027	
<i>Myrmica</i> -pontszám	kaszálás szeptemberben	-0,583	0,014	56,49%
	kaszálás májusban	-0,703	0,003	
	kaszálás májusban és szeptemberben	-0,657	0,006	
log(lepkeszám)	virágfejek száma	0,000026	0,286	53,18%
	<i>Myrmica</i> -pontszám	-0,033	0,077	

1. táblázat: A lineáris kevert modellek eredményei. A kaszálás típusánál a kontroll jelenti a referenciaszintet. Az utolsó oszlop értékei azt fejezik ki, hogy a random faktor hány százalékát magyarázza az összvarianciának. A szignifikáns *p*-értékeket félkövéren szedtük.

Rét	Függő változó	χ^2	p -érték
1	Fogott lepkék száma	7,14	0,067
2	Fogott lepkék száma	12,62	0,006
3	Fogott lepkék száma	6,90	0,075
4	Fogott lepkék száma	7,02	0,071
1	Vérű virágfejek száma	10,23	0,017
2	Vérű virágfejek száma	8,19	0,042
2	Myrmica-pontszám	8,07	0,045

2. táblázat: A rétenként végzett Kruskal-Wallis tesztek eredményei. Csak a szignifikáns és marginálisan szignifikáns eredményeket tüntettük fel. Magyarázó változó minden esetben a kaszálás típusa volt.



1. ábra: A szignifikáns Kruskal-Wallis tesztekhez használt adatok boxplot diagramja. A kaszálás típusát a mintavétel pillanatáig végzett kaszálások számával jelöltük (0: kontroll, 1: szeptemberi, 2: májusi, 3: májusi és szeptemberi kaszálás.)

Térkép a mintavételi területekről online elérhető itt:

<http://maps.google.com/maps/ms?hl=hu&ie=UTF8&oe=UTF8&msa=0&msid=116279886275538207121.00045ca935754c7b3aa4e>

Effects of mowing on populations of the scarce large blue butterfly
(*Maculinea teleius*) in SW Hungary

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Maculinea species are widely known of their obligate myrmecophilous life history and they enjoy special attention in nature conservation in Europe. Therefore, much more effort should be made in order to maintain their habitats in Hungary. We started a long-term habitat management experiment in SW Hungary in the Őrség National Park in 2007 to provide a scientific background for the maintenance of the scarce large blue's habitats. To study the effects of mowing, we designated four stripes of different mowing regimes on each of the four meadows along the Szentgyörgyvölgyi stream. The four types were mown in May, in

September, in May and in September, and there was an unmown control. Within the stripes, adjacent quadrates were designated and the abundance of both the butterflies and the food plant (*Sanguisorba officinalis*) and the frequency of host ants (*Myrmica spp.*) were surveyed in the flight period. Despite the differences between meadows in the management history and vegetation structure, we found similar effects of mowing: the abundance of the butterfly and the food plant were higher in the more intensively mown parts, while host ant frequency was higher in the less intensively mown areas. The latter areas may thus serve as refuges for ant colonies and their maintenance is essential for the persistence of the butterfly. Our results emphasize that a mosaic-like mowing scheme is essential for the survival of *Maculinea* butterflies and is probably important for many other species living in the same habitats.

Keywords: biodiversity, foodplant, grassland management, mowing, myrmecophily, *Myrmica*, social parasitism, host ant