Acta Zoologica Academiae Scientiarum Hungaricae 54 (3), pp. 257–268, 2008

HOST ANT USE OF *MACULINEA TELEIUS* IN THE CARPATHIAN BASIN (LEPIDOPTERA: LYCAENIDAE)

TARTALLY, A. and VARGA, Z.

Department of Evolutionary Zoology and Human Biology, University of Debrecen
H-4032, Egyetem tér 1, Debrecen, Hungary, E-mail: tartally@gmail.com

Host ant use of *Maculinea teleius* was investigated in 17 Hungarian and three Transylvanian (Romania) sites by opening *Myrmica* ant nests. A total of 856 nests of nine *Myrmica* species (*M. gallienii*, *M. rubra*, *M. ruginodis*, *M. sabuleti*, *M. salina*, *M. scabrinodis*, *M. schencki*, *M. specioides* and *M. vandeli*) were found and nests of six species (*M. gallienii*, *M. rubra*, *M. salina*, *M. scabrinodis*, *M. specioides* and *M. vandeli*) contained 114 *M. teleius* specimens in total. *M. rubra* and *M. scabrinodis* were the most frequently used host ants. *M. rubra* appeared to be more suitable in the western while *M. scabrinodis* proved to be more important in the eastern sites. *M. gallienii* and *M. salina* were only locally important hosts on a few sites. *M. specioides* and *M. vandeli* were parasitized only once. Five *Myrmica* nests also contained larvae of other *Maculinea* species. These results show a less restricted host ant use of *M. teleius* in the central part of the Carpathian Basin than records from France. Our results correspond with the host ant use data recorded from Poland.

Key words: Hungary, *Maculinea teleius*, *Myrmica*, social parasitism, Transylvania

INTRODUCTION

Larvae of the Scarce Large Blue butterfly, *Maculinea teleius* (BERGSTRÄSSER, 1779), have a socially parasitic life-cycle. They start their development by feeding on seeds in the flower heads of the host plant *Sanguisorba officinalis* L. A few weeks later, in their last, fourth instar, they descend to the ground. This is one of the most critical periods of their life-cycle when they need to be adopted by a suitable host ant colony. It requires not only a tolerant host ant colony but also a nest which contains enough brood because, after leaving the host plant, larvae of *M. teleius* are predators of the ant brood (e.g. THOMAS *et al.* 1989, WYNHOFF 2001, THOMAS & SETTELE 2004). Different *Myrmica* LATREILLE, 1804 species and *Aphaenogaster japonica* (Hymenoptera: Formicidae) have been reported as host ants of *M. teleius* from different regions (Table 1 and references therein). It is important therefore to identify the local host ant species of this vulnerable butterfly for its conservation (MUNGUIRA & MARTÍN 1999, SETTELE *et al.* 2005, IUCN 2006), and also because it can help shed light on the evolution of this type of parasitic interaction (ELMES *et al.* 1998, ALS *et al.* 2004).

Our aim was to investigate the host ant use of *M. teleius* in the central part of the Carpathian Basin. The current paper presents primarily unpublished data, complementary to our initially reported results (TARTALLY & CSŐSZ 2004, TARTALLY 2005*a, b*, TARTALLY & VARGA 2005*a, b*, TARTALLY *et al.* in press).

MATERIALS AND METHODS

The host ant use of *M. teleius* was investigated in 20 sites (Fig. 1, Table 2). Three of these were in Transylvania, Romania (Fânaţele Clujului: 23°37'N, 46°51'E; Răscruci: 46°54'N, 23°47'E; and Şardu: 46°52'N, 23°24'E) and 17 in Hungary (Aggtelek: 48°28'N, 20°30'E; Drahos-rét: 48°34'N, 21°26'E; Drávaiványi: 45°50'N, 17°49'E; Fülesd: 48°01'N, 22°38'E; Gödörháza: 46°45'N, 16°21'E; Gyertyánkúti-rétek: 48°29'N, 21°22'E; Hetefejércse: 48°08'N, 22°29'E; Hidegség: 47°23'N, 16°27'E; Ipolytarnóc: 48°14'N, 19°37'E; Kercaszomor: 46°46'N, 16°18'E; Kétvölgy: 46°53'N, 16°12'E; Lászlótanya: 46°33'N, 16°12'E; Meszes: 48°27'N, 20°47'E; Nógrádszakál: 48°12'N, 19°32'E; Őriszentpéter: 46°51'N, 16°12'E; Velemér: 46°44'N, 16°21'E; Vörös-rét: 47°46'N, 17°42'E). To obtain data on host ant use, *Myrmica* nests were carefully opened (usually without full excavation, to minimize disturbance) and the number of *M. teleius* larvae, pupae or exuvia (= 'specimens' in the following) present was recorded. Nests exclusively within 2 m of *S. officinalis* host plants were chosen as this is the approximate foraging zone of *Myrmica* workers, and nests farther from the host plants are unlikely to adopt *Maculinea* larvae (ELMES *et al.* 1998). Investigations were usually completed in the early flying period (late July – early August) between 2000 and 2007. However, we did the investigation about one month before the flying period on sites (see TARTALLY & VARGA 2005*a*, TARTALLY *et al.* 2008) where *M. teleius* and *M. nausithous* (BERGSTRÄSSER, 1779) co-occurred, because pupae of these two butterflies are rather similar (but pupae of *M. alcon* ([DENIS et SCHIFFERMÜLLER], 1775) are different from them (see ŚLIWIŃSKA *et al.* 2006). By this method we did not find pupae, only prepupal larvae, and the identification of *Maculinea* larvae is

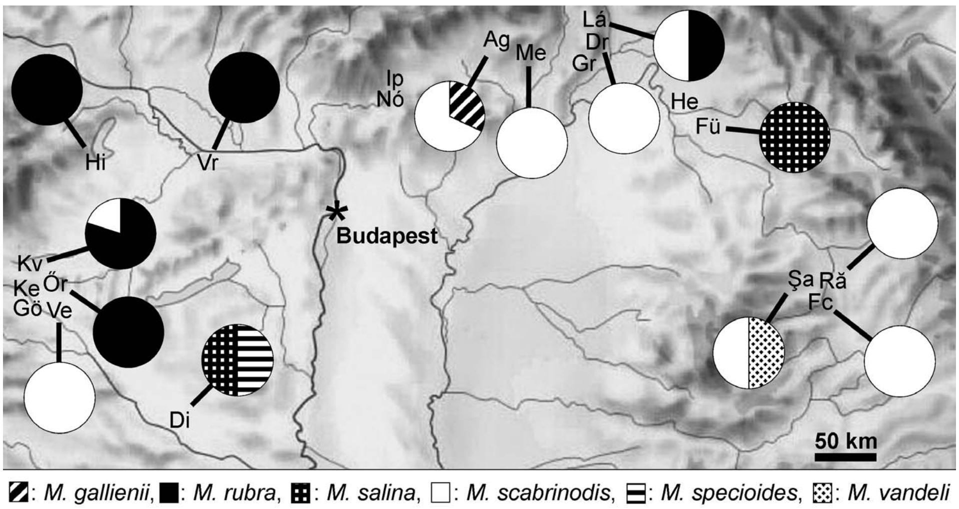

Fig. 1. The investigated sites and the proportion of *M. teleius* specimens found in nests of different *Myrmica* species (see Table 2 for more details and for a key to site codes)

Table 1. Recorded host ants of *M. teleius* from the most intensively studied regions (references in parentheses: 1: YAMAGUCHI 1988, 2: THOMAS *et al.* 1989, 3: ELMES *et al.* 1998, 4: STANKIEWICZ & SIELEZNIEW 2002, 5: BUSZKO *et al.* 2005, 6: WITEK *et al.* 2005, 7: WOYCIECHOWSKI *et al.* 2006, 8: this paper; for a more detailed review: ALS *et al.* 2004: Supplementary table 10, FIEDLER 2006: Digital supplementary material, PECH *et al*. 2007: Table 1, 5).

Recorded host ants	Hungary (8)	Japan (1)	Mongolia (7)	Romania (8)	Poland (4, 5, 6)	Poland & France (2, 3)
Aphaenogaster japonica FOREL, 1911		+				
Myrmica angulinodis RUZSKY, 1905			+			
M. forcipata KARAVAIEV, 1931			+			
M. gallienii BONDROIT, 1919	+				+	
M. kamtschatica KUPYANSKAYA, 1986			+			
M. kurokii FOREL, 1907						
M. lobicornis NYLANDER, 1846						
M. rubra (LINNAEUS, 1758)	+				+	+
M. ruginodis NYLANDER, 1846		+			+	
M. rugulosa NYLANDER, 1846					+	
M. sabuleti MEINERT, 1860						+
M. salina RUZSKY, 1905	+					
M. scabrinodis NYLANDER, 1846	+			+	+	+
M. specioides BONDROIT, 1918	+					
M. vandeli BONDROIT, 1920	+			+		+

Table 2. The number of *Myrmica* nests found and their recorded use by *M. teleius* in the investigated sites (see also Fig. 1); Two measures of hosts specificity arte given: P1 is the 2-tailed probability from the Fisher exact test of heterogeneity in infection of host ant nests. P2 is the probability from a randomization test of ant nests between species (see Materials and Methods).

Site (code on Fig. 1)	*Myrmica*	Sample size	Infested with *M. teleius*	Total no. of *M. teleius*	Mean in examined nests	Mean in infested nests (range)	P1	P2
Aggtelek (Ag)	*M. gallienii*	17	2 (11.8 %)	7	0.41	3.5 (1–6)	0.759	0.568
	M. sabuleti	2						
	M. scabrinodis	78	6 (7.7 %)	15	0.19	2.5 (1–4)		
	M. schencki	2						
	M. vandeli	1						
Drahos-rét (Dr)	*M. scabrinodis*	53	2 (3.8 %)	2	0.04	1	1.00	0.602
	M. vandeli	19						
Drávaiványi (Di)	*M. salina*	1	1 (100.0 %)	1	1.00	1		
	M. specioides	1	1 (100.0 %)	1	1.00	1		
Fânațele Clujului (Fc)	*M. scabrinodis*	58	1 (1.7 %)	1	0.02	1		
Fülesd (Fü)	*M. gallienii*	6					0.410	0.494
	M. ruginodis	2						
	M. salina	15	3 (20.0 %)	5	0.33	1.7 (1–3)		
	M. scabrinodis	9						
Gödörháza (Gö)	*M. rubra*	4						
	M. ruginodis	1						
	M. scabrinodis	36						
Gyertyánkúti-rétek (Gr)	*M. ruginodis*	1						
	M. scabrinodis	9						
	M. vandeli	4						
Hetefejércse (He)	*M. scabrinodis*	5						
Hidegség (Hi)	*M. rubra*	8	3 (37.5 %)	17	2.13	5.7 (1–8)		

Table 2 (continued)

Site (code on Fig. 1)	*Myrmica*	Sample size	Infested with *M. teleius*	Total no. of *M. teleius*	Mean in examined nests	Mean in infested nests (range)	P1	P2
Ipolytarnóc (Ip)	*M. gallienii*	6						
	M. rubra	10						
	M. ruginodis	2						
	M. scabrinodis	15						
Kercaszomor (Ke)	*M. rubra*	11						
	M. scabrinodis	37						
Kétvölgy (Kv)	*M. gallienii*	1					1.00	1.00
	M. rubra	14	1 (7.1 %)	8	0.57	8		
	M. scabrinodis	11	1 (9.1 %)	2	0.18	2		
	M. specioides	1						
Lászlótanya (Lá)	*M. rubra*	2	1 (50.0 %)	2	1.00	2	0.263	0.075
	M. scabrinodis	27	2 (7.4 %)	2	0.07	1		
Meszes (Me)	*M. rubra*	2					1.00	1.00
	M. scabrinodis	200	21 (10.5 %)	31	0.16	1.5 (1–4)		
Nógrádszakál (Nó)	*M. rubra*	7						
	M. scabrinodis	10						
Őriszentpéter (Őr)	*M. rubra*	21	1 (4.8 %)	1	0.05	1	1.00	1.00
	M. scabrinodis	10						
Răscruci (Ră)	*M. scabrinodis*	49	12 (24.5 %)	14	0.29	1.2 (1–2)		
Şardu (Şa)	*M. scabrinodis*	26	1 (3.8 %)	1	0.04	1	1.00	1.00
	M. vandeli	21	1 (4.8 %)	1	0.05	1		
Velemér (Ve)	*M. gallienii*	1					1.00	1.00
	M. rubra	6						
	M. scabrinodis	13	1 (7.7 %)	1	0.08	1		
Vörös-rét (Vr)	*M. rubra*	7	2 (28.6 %)	2	0.29	1	0.195	0.1998
	M. ruginodis	1						
	M. scabrinodis	13						

straightforward (ŚLIWIŃSKA *et al.* 2006). These larvae had obviously spent the winter in their host nests, surviving a critical period of their lives (ELMES *et al.* 2004). The number and species of *Maculinea* larvae found was noted after determination using a 20× hand lens in the field. Five to ten workers were collected from each *Myrmica* nest opened, and were preserved in 67% ethanol for identification in the laboratory (using keys in SEIFERT 1988).

To quantify the host ant specificity, the heterogeneity of the number of *M. teleius* specimens between nests of different species was compared using two methods. First, a Fisher exact test was used to compare the observed number of infected nests with the number expected if they were infected at random. Second, a Chi-squared statistic was computed comparing the number of *M. teleius* specimens observed with the number expected based on the number of nests available. The significance of this was tested by reassigning each nest (and its associated number of *M. teleius* specimens) randomly to one of the *Myrmica* species observed at a site 100000 times (using the software program MacSamp: NASH 2007), with the constraint that the total number of nests of each species was the same as that observed. This gives a measure of the host specificity of the *Maculinea* at a site based on the observed distribution of *Maculinea* between nests, but the power of this test to detect heterogeneity in the distribution between ant species is low except for those cases in which many ant nests have been investigated.

The overall distribution of *M. teleius* specimens within nests was compared between species using the 'MASS' package (version 7.2–36) of the software package 'R' (version 2.5.1; http://www.R-project.org) to perform tests that are the equivalent of General Linear Models with negative binomial errors.

RESULTS

A total of 856 nests of nine *Myrmica* species (*M. gallienii*, n = 31; *M. rubra*, n = 92; *M. ruginodis*, n = 7; *M. sabuleti*, n = 2; *M. salina*, n = 16; *M. scabrinodis*, n = 659; *M. schencki*, n = 2; *M. specioides*, n = 2; *M. vandeli*, n = 45) were investigated within 2 m from the *S. officinalis* host plants at the 20 sites (Table 2). In total 114 *M. teleius* specimens were found in 63 nests of six *Myrmica* species (*M. gallienii*, *M. rubra*, *M. salina*, *M. scabrinodis*, *M. specioides* and *M. vandeli*) in 14 sites. Nests of *M. ruginodis*, *M. sabuleti* and *M. schencki* were not found to be infested. Overall, two thirds of the *Myrmica* species examined were used as hosts, and 7.4% of all nests were infested (Table 2).

Five *Myrmica* nests also contained larvae of other *Maculinea* species besides *M. teleius*: one *M. rubra* nest also contained larvae of *M. nausithous* (Kétvölgy: 8 *M. teleius* + 28 *M. nausithous*; TARTALLY & VARGA 2005*a*), one *M. scabrinodis* nest likewise contained larvae of *M. nausithous* (Răscruci: 1 *M. teleius* + 1 *M. nausithous*, TARTALLY *et al.* 2008) and three *M. scabrinodis* nests contained larvae of *M. alcon*, too (Răscruci: 1 *M. teleius* + 1 *M. alcon*, 1 *M. teleius* + 1 *M. alcon*, 1 *M. teleius* + 5 *M. alcon*; A. TARTALLY, unpublished data). It should be noted that other *M. nausithous* and *M. alcon* specimens were also found during our surveys in *M. teleius* sites (TARTALLY & CSŐSZ 2004, TARTALLY 2005*a, b*, TARTALLY & VARGA 2005*a, b*, TARTALLY *et al.* 2008; A. TARTALLY, unpublished data).

The distribution of *M. teleius* specimens found in nests of different *Myrmica* species was well described by a negative binomial distribution (GLM with negative binomial errors and log-link; dispersion parameter k = 0.194: Goodness of fit test; Pearson $\chi^2 = 628.3$, d.f. = 822, $p = 0.999$), and differed significantly between sites (change in deviance = 84.56, d.f. = 19, $p < 0.001$), but not between host species (change in deviance = 11.81, d.f. = 8, $p = 0.160$; Fig. 2). When the analysis was repeated with only the two most frequently found and infested *Myrmica* species, it became clear that *M. rubra* was significantly more suitable for *M. teleius* than *M. scabrinodis* (k = 0.196: between sites; change in deviance = 77.45, d.f. = 18, $p < 0.001$: between ant species; change in deviance = 4.37, d.f. = 1, $p = 0.036$).

No population showed significant heterogeneity in host ant use, although Lászlótanya approached significance when the heterogeneity of the number of *M. teleius* specimens in the nests of different *Myrmica* species was compared (Table 2).

DISCUSSION

To our knowledge, this is the first study to focus directly on the host ant use of *M. teleius* in south-eastern Central Europe (although there are some results initially published in papers concentrating on other *Maculinea* species: TARTALLY & CSŐSZ 2004, TARTALLY 2005*a, b*, TARTALLY & VARGA 2005*a, b*, VÁLYI NAGY & CSŐSZ 2007, TARTALLY *et al.* 2008; see also BATÁRY *et al.* 2007). While the number of infested nests found in a site (Table 2) is usually too small to draw strong conclusions about host ant specificity, there are some general patterns.

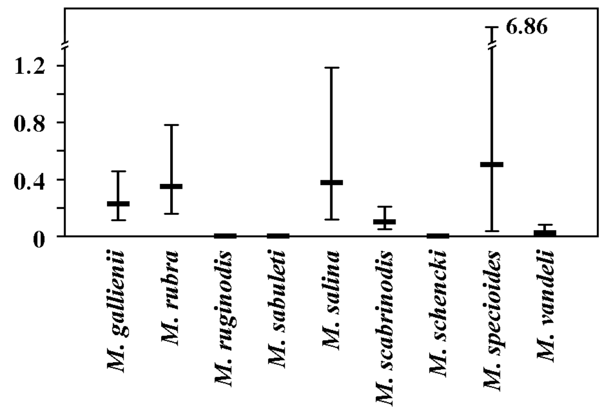

Fig. 2. The mean number (± SE) of *M. teleius* specimens found in nests of the different *Myrmica* ant species combining all data. Standard errors are based on a General Linear Model with negative binomial errors (k = 0.194) and log-link, and so are asymmetrical

M. teleius was found with six *Myrmica* species (*M. gallienii*, *M. rubra*, *M. salina*, *M. scabrinodis*, *M. specioides* and *M. vandeli*) therefore this butterfly appears not to have strict host ant specificity in the Carpathian Basin. However, it can be contrasted with the strict host ant specificity (to *M. scabrinodis*) initially found in some French and Polish sites (THOMAS *et al.* 1989, ELMES *et al.* 1998). Later these original results from Poland were supplemented with more data (STANKIEWICZ & SIELEZNIEW 2002, BUSZKO *et al.* 2005, WITEK *et al.* 2005) and it is now clear that the host ant use of *M. teleius* is more complex there (Table 1).

If we follow the criteria (see ALS *et al.* 2004: supplementary table 10) that 'primary hosts' raise more than 10% of specimens in a population, it could be concluded that all the recorded host ant species would be 'primary hosts' in the different sites (Fig. 1, Table 2). Nevertheless, we should be careful with this statement because the number of *M. teleius* specimens recorded in a site was usually too low (more than 10 would be needed) for such a calculation (Table 2). Combining our data (see Results), we found only two ant species in the Carpathian Basin which reared more than 10% of *M. teleius* specimens found across the investigated sites (*M. rubra*, 26.3%; *M. scabrinodis*, 60.5%). This is not surprising because these two *Myrmica* species were the most often recorded host ants (see Results and Table 2).

There were differences in the mean numbers of *M. teleius* specimens found in the nests of the different *Myrmica* species when the data were combined (Fig. 2), and this number was significantly higher for *M. rubra* than for *M. scabrinodis* when only these two major hosts were examined. Interestingly, *M. rubra* appeared to be more suitable in the western sites while *M. scabrinodis* proved to be more important in the eastern sites (Fig. 1, Table 2). This phenomenon is simple to explain since *M. rubra* is usually rare or missing from the eastern sites (Table 2). Moreover, this ant usually forms larger colonies than *M. scabrinodis* (SEIFERT 1988) and therefore an average *M. rubra* nest can rear more *Maculinea* larvae (e.g. the infested *M. rubra* nest at Kétvölgy contained not only eight *M. teleius* but also 28 *M. nausithous* larvae which is an exceptionally high number of predatory *Maculinea* larvae within the same nest; see TARTALLY & VARGA 2005*a*). Thus, it is not surprising that *M. rubra* was significantly more suitable for *M. teleius* than *M. scabrinodis* (see Results, Fig. 2).

In Poland, *M. scabrinodis* was regarded as the primary host ant of *M. teleius* for a long time (THOMAS *et al.* 1989, ELMES *et al.* 1998) but recent results show that *M. rubra*, if common on a site, is often a significantly more suitable host of *M. teleius* there (STANKIEWICZ & SIELEZNIEW 2002, see also BUSZKO *et al.* 2005, WITEK *et al.* 2005). The fact that *M. gallienii* was found to be an important host ant of *M. teleius* on sites in both countries is another similarity between Poland and Hungary (at Kosyń in Poland: STANKIEWICZ & SIELEZNIEW 2002; at Aggtelek in

Hungary: Fig. 1, Table 2). However, there were four Hungarian sites where *M. gallienii* was also recorded (Table 2) but was not found to be infested.

The situation seems to be different in the case of *M. salina*. This species was recorded in two Hungarian sites and it reared *M. teleius* at both of them (Fig. 1, Table 2). Interestingly, *M. salina* was the only recorded host ant at Fülesd, where nests of *M. scabrinodis* and *M. gallienii* (both of which are hosts in NE Hungary, Fig. 1, Table 2) were not found to be infested. It would be interesting to obtain more data from this site to investigate whether there is a similarly strong adaptation of *M. teleius* to *M. salina* as was found to be the case for *M. alcon* on the same site (see TARTALLY 2005*a*). One nest of *M. specioides* (from two nests in two sites) and another of *M. vandeli* (from 45 nests in four sites) were also found to be infested by *M. teleius* (Fig. 1, Table 2). *M. vandeli* has already been recorded as a host of *M. teleius* (one nest with one specimen from France or Poland; THOMAS *et al.* 1989, ELMES *et al.* 1998), however, as far as we know, *M. specioides* and *M. salina* have not been recorded as hosts of *M. teleius* outside Hungary (Table 1 and references therein).

The three *Myrmica* species not infested were among the rarest species in the survey (there were only seven *M. ruginodis*, two *M. sabuleti* and two *M. schencki* nests recorded in total; Table 2), which is consistent with the possibility that this is due to the low level of "sampling" of these species, but this effect may also be of importance for the butterflies themselves, if these *Myrmica* species are consistently rare. This is easily imaginable because there were no significant deviations from random distribution amongst ant species when the heterogeneity of the number of *M. teleius* specimens in the nests of different *Myrmica* species was compared in the different sites (Table 2).

The other two *Maculinea* species (*M. alcon* and *M. nausithous*) inhabiting marshy meadows often co-occur and have common host ants (and even commonly parasitized nests, see Results) with *M. teleius* in Hungary and Transylvania. For example, *M. teleius* and *M. alcon* commonly use *M. salina* at Fülesd, *M. vandeli* at Şardu and *M. scabrinodis* at Drahos-rét, Răscruci and Şardu (TARTALLY *et al.* 2008, TARTALLY 2005*a*, A. TARTALLY, unpublished data, Fig. 1, Table 2); *M. teleius* and *M. nausithous* commonly use *M. scabrinodis* at Răscruci and *M. rubra* at Hidegség and Kétvölgy (TARTALLY *et al.* 2008, TARTALLY & VARGA 2005*a*). These contrast with results from Western Europe, where each *Maculinea* species depends on a single, and different, *Myrmica* species (THOMAS *et al.* 1989, ELMES *et al.* 1998).

It requires further investigation to determine if the differences between the host ant use of *M. teleius* on different sites simply reflects host ant availability, whether there is a coevolutionary mosaic of adaptation to local hosts (sensu

THOMPSON 1999), or some other explanations (see THOMAS *et al.* 2005). Moreover, it would be useful to get information on the host ant specificity of *M. teleius* from further western Central European regions (not only from France; THOMAS *et al.* 1989, ELMES *et al.* 1998) and so determine if the strength of host ant specificity is generally higher there than it was found in eastern Central Europe (in Poland and Hungary; THOMAS *et al.* 1989, ELMES *et al.* 1998, STANKIEWICZ & SIELEZNIEW 2002, BUSZKO *et al.* 2005, WITEK *et al.* 2005, this paper). It would be particularly interesting to test whether the number of host ant species of *M. teleius* declines towards the western parts of Europe, because the genus *Maculinea* is thought to have evolved in continental East Asia (SIBATANI *et al.* 1994) and European populations therefore can be considered peripheral. Similar phenomena are well known in the host plant specificity of polyphagous butterflies (e.g. DE LATTIN 1967, MARTIN & PULLINS 2004, SCHMIDT & HUGHES 2006). Moreover, to answer this problem, it would be useful to get more knowledge about the host ant use of *M. teleius* in Asia because the scarce available data (Table 1 and references therein) suggest that there is little host ant specificity there.

The multiple host ant use of *M. teleius* found in Hungary and Transylvania could suggest that this butterfly can easily adapt to some new host ant species when circumstances (e.g. from human disturbance) change. However, we should be careful with such interpretations based on the currently limited amount of data available.

*

Acknowledgements – We would like to thank A. AMBRUS, M. GOIA, P. KOZMA, L. RÁKOSY, B. SZŰCS, E. TÓTH, and T.-CS. VIZAUER for assisting us with fieldwork and E. TÓTH and B. SZŰCS for revising an earlier version of the manuscript. An anonymous referee suggested valuable changes and D. R. NASH helpfully discussed some problems and introduced us to the MacSamp software (NASH 2007). Research has been funded by the EC within the RTD project "MacMan" (EVK2-CT-2001-00126; SETTELE *et al.* 2002) and by grants from the National Office for Research and Technology (NKFP-3B/023/2004).

REFERENCES

ALS, T. D., VILA, R., KANDUL, N. P., NASH, D. R., YEN, S.-H., HSU, Y.-F., MIGNAULT, A. A., BOOMSMA, J. J. & PIERCE, N. E. (2004) The evolution of alternative parasitic life histories in Large Blue butterflies. *Nature* **432**: 386–390.

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

BUSZKO, J., SIELEZNIEW, M. & STANKIEWICZ, A. M. (2005) The distribution ad ecology of Maculinea teleius and M. nausithous in Poland. Pp. 210–213. *In:* SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds) (2005) *Studies on the ecology and conservation of butterflies in Europe*

Vol. 2: Species ecology along a European gradient: Maculinea butterflies as a model. Pensoft, Sofia.

DE LATTIN, G. (1967) *Grundriss der Zoogeographie.* Hochschullehrbücher für Biologie 12. Fischer G. Verlag, Stuttgart, 602 pp.

ELMES, G. W., THOMAS, J. A., WARDLAW, J. C., HOCHBERG, M., CLARKE, R. T. & SIMCOX, D. J. (1998) The ecology of Myrmica ants in relation to the conservation of Maculinea butterflies. *Journal of Insect Conservation* **2**: 67–78.

ELMES, G. W., WARDLAW, J. C., SCHÖNROGGE, K. & THOMAS, J. A. (2004) Food stress causes differential survival of socially parasitic larvae of Maculinea rebeli (Lepidoptera, Lycaenidae) integrated in colonies of host and non-host Myrmica species (Hymenoptera, Formicidae). *Entomologia Experimentalis et Applicata* **110**: 53–63.

FIEDLER, K. (2006) Ant-associates of Palaerctic lycaenid butterfly larvae (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae) – a review. *Myrmecologische Nachrichten* **9**: 77–87.

IUCN (2006) *IUCN Red List of threatened species*. <www.iucnredlist.org>. Downloaded on 29 August 2007.

MARTIN, L. A. & PULLIN, A. S. (2004) Host-plant specialisation and habitat restriction in an endangered insect, Lycaena dispar batavus (Lepidoptera: Lycaenidae) I. Larval feeding and oviposition preferences. *European Journal of Entomology* **101**: 51–56.

MUNGUIRA, M. L. & MARTÍN, J. (eds) (1999) *Action Plan for the Maculinea butterflies in Europe.* Nature and Environment, No. 97. Council of Europe Publishing, Strasbourg, 64 pp.

NASH, D. R. (2007) *MacSamp* (version: 1.0.0.15) <http://www.zi.ku.dk/personal/drnash/download/MacSamp.html>. Downloaded on 08 October 2007.

PECH, P., FRIC, Z. & KONVICKA, M. (2007) Species-specificity of the Phengaris (Maculinea) – Myrmica host system: Fact or myth? (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae). *Sociobiology* **50**: 983–1003.

RADCHENKO, A., ELMES, G. W., CZECHOWSKA, W., STANKIEWICZ, A., CZECHOWSKI, W. & SIELEZNIEW, M. (2003) First records of Myrmica vandeli Bondroit and M. tulinae Elmes, Radchenko et Aktaç (Hymenoptera: Formicidae) for Poland, with a key for the scabrinodis- and sabuleti-complexes. *Fragmenta Faunistica* **46**: 47–57.

SCHMIDT, D. J. & HUGHES, J. M. (2006) Genetic affinities among subspecies of a widespread Australian lycaenid butterfly, Ogyris amaryllis (Hewitson). *Australian Journal of Zoology* **54**: 429–446.

SEIFERT, B. (1988) A taxonomic revision of the Myrmica species of Europe, Asia Minor and Caucasica (Hymenoptera, Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz* **62**: 1–75.

SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds) (2005) *Studies on the ecology and conservation of butterflies in Europe Vol. 2: Species ecology along an European gradient: Maculinea butterflies as a model.* Pensoft, Sofia. 289 pp.

SETTELE, J., THOMAS, J. A., BOOMSMA, J., KUEHN, E., NASH, D. R., ANTON, C., WOYCIECHOWSKI, M. & VARGA, Z. (2002) MACulinea butterflies of the habitats directive and European red list as indicators and tools for conservation and MANagment (MacMan). *Verhandlungen der Gesellschaft für Ökologie* **32**: 63.

SIBATANI, A., SAIGUSA, T. & HIROWATARI, T. (1994) The genus Maculinea van Eecke, 1915 (Lepidoptera: Lycaenidae) from the East Palaearctic Region. *Tyô to Ga* **44**: 157–220.

ŚLIWIŃSKA, E. B., NOWICKI, P., NASH, D. R., WITEK, M., SETTELE, J. & WOYCIECHOWSKI, M. (2006) Morphology of caterpillars and pupae of European Maculinea species (Lepidoptera: Lycaenidae). *Entomologica Fennica* **17**: 351–358.

STANKIEWICZ, A. & SIELEZNIEW, M. (2002) Host specificity of Maculinea teleius Bgstr. and M. nausithous Bgstr. (Lepidoptera: Lycaenidae) the new insight. *Annales Zoologici* **52**: 403–408.

TARTALLY, A. (2005*a*) Myrmica salina (Hymenoptera: Formicidae) as a host of Maculinea alcon (Lepidoptera: Lycaenidae). *Sociobiology* **46**: 39–43.

TARTALLY, A. (2005*b*) Neotypus melanocephalus (Hymenoptera: Ichneumonidae): the first record of a parasitoid wasp attacking Maculinea teleius (Lycaenidae). *Nota Lepidopterologica* **28**: 65–67.

TARTALLY, A. & CSŐSZ, S. (2004) Adatok a Maculinea boglárkalepkék (Lepidoptera: Lycaenidae) kárpát-medencei hangyagazdáiról. [Data on the ant hosts of the Maculinea butterflies (Lepidoptera: Lycaenidae) of Hungary.] *Természetvédelmi Közlemények* **11**: 309–317.

TARTALLY, A., RÁKOSY, L., VIZAUER, T.-CS., GOIA, M. & VARGA, Z. (2008) Maculinea nausithous exploits Myrmica scabrinodis in Transylvania: unusual host ant species of a myrmecophilous butterfly in an isolated region. *Sociobiology* **51**[in press]

TARTALLY, A. & VARGA, Z. (2005*a*) Myrmica rubra (Hymenoptera: Formicidae): the first data on host-ant specificity of Maculinea nausithous (Lepidoptera: Lycaenidae) in Hungary. *Myrmecologische Nachrichten* **7**: 55–59.

TARTALLY, A. & VARGA, Z. (2005*b*) Host-ant specificity of Maculinea species in Hungary, connections with parasitoids and host plants. Pp. 94–98. *In:* SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds) (2005) *Studies on the ecology and conservation of butterflies in Europe Vol. 2: Species ecology along a European gradient: Maculinea butterflies as a model.* Pensoft, Sofia.

THOMAS, J. A., ELMES, G. W., SCHÖNROGGE, K., SIMCOX, D. J. & SETTELE, J. (2005) Primary hosts, secondary hosts and 'non-hosts': common confusions in the interpretation of host specificity in Maculinea butterflies and other social parasites of ants. Pp. 99–104. *In:* SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds) (2005) *Studies on the ecology and conservation of butterflies in Europe Vol. 2: Species ecology along a European gradient: Maculinea butterflies as a model.* Pensoft, Sofia.

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

THOMAS, J. A. & SETTELE, J. (2004) Butterfly mimics of ants. *Nature* **432**: 283–284.

THOMPSON, J. N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *The American Naturalist* **153**: S1-S14.

VÁLYI NAGY, M. & CSŐSZ, S. (2007) Host ant specificity of the Large Blue butterfly, Maculinea alcon (Denis & Schiffermüller, 1775), in the Carpathian Basin (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae). *Myrmecological News* **10**: 124.

WITEK, M., NOWICKI, P., SKÓRSKA, P., SLIWINSKA, E. & WOYCIECHOWSKI, M. (2005) Host ant specificity and integration rate with Myrmica ants in larvae of Maculinea teleius butterflies. Pp. 105–106. *In:* SETTELE, J., KÜHN, E. & THOMAS, J. A. (eds) (2005) *Studies on the ecology and conservation of butterflies in Europe Vol. 2: Species ecology along a European gradient: Maculinea butterflies as a model.* Pensoft, Sofia.

WOYCIECHOWSKI, M., SLOWIK, J. & MUEHLENBERG, M. (2006) Hosts of the butterfly, Maculinea teleius, among Myrmica ants in Northern Mongolia (Lepidoptera: Lycaenidae; Hymenopera: Formicidae). *Sociobiology* **48**: 493–502.

WYNHOFF, I. (2001) *At home on foreign meadows: the reintroduction of two Maculinea butterfly species*. Published PhD thesis, Wageningen Agricultural University, Wageningen, 236 pp.

YAMAGUCHI, S. (1988) *The life histories of five myrmecophilous lycaenid butterflies of Japan.* Kodansha, Japan.

Revised version received September 5, 2007, accepted December 3, 2007, published September 10, 2008