

# Species-Specificity of the *Phengaris* (*Maculinea*) – *Myrmica* Host System: Fact or myth? (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae)

by

Pavel Pech<sup>1,2\*</sup>, Zdenek Fric<sup>1,3</sup> & Martin Konvicka<sup>1,2</sup>

## ABSTRACT

*Phengaris* butterflies, which is the valid name for *Maculinea* van Eecke, 1915, display an intricate parasitic relationship with *Myrmica* ants. The relationship was long believed to be non-specific, so that each *Phengaris* could develop in many *Myrmica* species, but since an influential paper by Thomas *et al.* (1989), there was a shift towards viewing it as a specific system. We review existing information to assess two currently prevailing hypotheses, the species-specificity hypothesis (each *Phengaris* utilises a single primary host), and local specificity hypothesis (the specificity exists on a finer, population-level basis). We show that the number of ant hosts per butterfly species tends to increase with the number of ant species examined. The cumulative number of ant hosts increases with the cumulative numbers of ants surveyed in individual studies in three European *Phengaris* taxa (*P. teleius*, *P. alcon*, *P. rebeli*), but not in *P. arion* and *P. nausithous*. Local specificity applies only for some populations, mainly of *P. alcon*, and seems to prevail near the edge of butterfly species' ranges. We conclude that both species-specificity and local specificity of the *Phengaris* – *Myrmica* relationships are poorly supported at present. Some of the cases of strict species-to-species relationships may represent an apparent specialization due to limited *Myrmica* species pools near range edges of individual *Phengaris* (or *Myrmica*) species. Although more detailed surveys across entire ranges of individual *Phengaris* species are necessary, it is often

---

<sup>1</sup>Department of Ecology and Conservation Biology, Centre of Biology, Institute of Entomology, Branisovska 31, CZ-37005 Ceske Budejovice, Czech Republic

<sup>2</sup>Department of Zoology, Faculty of Biological Sciences, University of South Bohemia, Branisovska 31, CZ-37005 Ceske Budejovice, Czech Republic

<sup>3</sup>Department of Theoretical Ecology, Institute of Systems Biology and Ecology, Czech Academy of Sciences, Na Sadkach 7, CZ-37005 Ceske Budejovice, Czech Republic

\* corresponding author. e-mail: pavel.pech@bf.jcu.cz

not necessary to know exact patterns of butterfly – ant associations in order to conserve and manage threatened populations of the butterflies. Populations of both ants and butterflies are ultimately affected by such factors as sward structure and microclimate, and these factors, rather than ant assemblages, are manipulated by site management.

Key words: *Lycaenidae*, *Formicidae*, conservation, ecology, myrmecophily, parasitism

## INTRODUCTION

Butterflies of the palaeartic genus *Phengaris* Doherty, 1891 (a valid name of *Maculinea* van Eecke, 1915, see Fric *et al.* 2007) (Lepidoptera: Lycaenidae) display an intricate association with ants. Young *Phengaris* caterpillars feed on reproductive tissues of a few plant species, while older larvae parasitise nests of the ant genus *Myrmica* (Hymenoptera: Formicidae) (Table 1). They either directly prey on ant brood (e.g. *P. arion*), are fed by workers via regurgitation (*P. alcon*), or display a transitional behavior (*P. nausithous*) (Als *et al.* 2004; Pech *et al.* 2004; Fric *et al.* 2007).

All *Phengaris* species are highly endangered in Europe. (Van Swaay & Warren 1999). The declines were caused by large-scale habitat loss due to agricultural intensification, such as drainage of wet grasslands and abandonment of traditional pastoral use of dry grasslands. Awareness of the declines led to legal protection of individual species by both national and EU legislation, intensive research onto their habitat requirements and general biology (e.g., Thomas & Elmes 1998; Als *et al.* 2004; Pech *et al.* 2004; Mouquet *et al.* 2005a,b; Settele *et al.* 2005), and to several reintroduction projects (Thomas 1995a,b; Wynhoff 1998; Munguira & Martín 1999). At present, the *Phengaris* – *Myrmica* system may represent the most intensively studied myrmecophilous relationship in the world.

This life history of *Phengaris* butterflies had been known for decades (Chapman 1916a,b), but it was long believed to be non-specific, existing on a generic level, so that any species of *Myrmica* could support development of any *Phengaris* (Malicky 1969). More detailed research has changed the view. Thomas *et al.* (1989) excavated a number of nests of all European species and presented evidence for highly exacting, species-to-species relationship between *Phengaris* and *Myrmica*. Each *Phengaris* species should specialise

Table 1. Records of *Phengaris caterpillars'* presence in *Myrmica* colonies

<i>Phengaris</i> species	Host ant	References
<i>P. alcon</i> (Denis & Schiffermüller, 1775)	<i>Myrmica ruginodis</i> Nylander, 1846	Thomas <i>et al.</i> 1989; Elmes <i>et al.</i> 1994; Als <i>et al.</i> 2002
	<i>M. rubra</i> (Linnaeus, 1758)	Thomas <i>et al.</i> 1989; Elmes <i>et al.</i> 1994; Als <i>et al.</i> 2002; Tartally & Varga 2005b
	<i>M. scabrinodis</i> Nylander, 1846	Elmes <i>et al.</i> 1994; Křenová <i>et al.</i> 2002; Sielezniew & Stankiewicz 2004; Tartally 2005a
<i>P. rebeli</i> (Hirsche, 1905)	<i>M. vandeli</i> Bondroit, 1920	Sielezniew & Stankiewicz 2004; Tartally & Varga 2005b
	<i>M. salina</i> Ruzsky, 1905	Tartally 2005a
	<i>Myrmica schenckii</i> Emery, 1984	Thomas <i>et al.</i> 1989; Steiner <i>et al.</i> 2003; Stankiewicz <i>et al.</i> 2005a, b; Tartally & Varga 2005b
	<i>M. sabuleti</i> Meinert, 1860	Fiedler 1989; Thomas <i>et al.</i> 1989; Steiner <i>et al.</i> 2003; Tartally & Varga 2005b
	<i>M. scabrinodis</i> Nylander, 1846	Fiedler 1989; Thomas <i>et al.</i> 1989; Steiner <i>et al.</i> 2003; Tartally & Varga 2005b
	<i>M. lonae</i> Finzi, 1926	Tartally & Varga 2005b
	<i>M. sulcinodis</i> Nylander, 1846	Fiedler 1989; Steiner <i>et al.</i> 2003
	<i>M. speciosoides</i> Bondroit, 1918	Steiner <i>et al.</i> 2003; Tartally & Varga 2005b
	<i>M. ruginodis</i> Nylander, 1846	Steiner <i>et al.</i> 2003
	<i>M. regulosa</i> Nylander, 1846	Stankiewicz <i>et al.</i> , 2005a
<i>P. teleius</i> (Bergsträsser, 1779)	<i>M. sabuleti</i> Meinert, 1860	Thomas <i>et al.</i> 1989
	<i>M. scabrinodis</i> Nylander, 1846	Malicky 1969; Thomas <i>et al.</i> 1989; Stankiewicz & Sielezniew 2002; Buszko <i>et al.</i> 2005; Tartally 2005b; Witek <i>et al.</i> 2005
	<i>M. rubra</i> (Linnaeus, 1758)	Thomas <i>et al.</i> 1989; Stankiewicz & Sielezniew 2002; Buszko <i>et al.</i> 2005; Tartally & Varga 2005a; Witek <i>et al.</i> 2005
	<i>M. vandeli</i> Bondroit, 1920	Thomas <i>et al.</i> 1989
	<i>M. salina</i> Ruzsky, 1905	Tartally 2005b
	<i>M. speciosoides</i> Bondroit, 1918	Tartally & Varga, 2005b
	<i>M. galliceni</i> Bondroit, 1919	Stankiewicz & Sielezniew 2002; Buszko <i>et al.</i> 2005
	<i>M. regulosa</i> Nylander, 1846	Witek <i>et al.</i> 2005
	<i>M. ruginodis</i> Nylander, 1846	Malicky 1969; Kawazoé <i>et al.</i> 1979; Fukuda <i>et al.</i> 1992; Sibatani <i>et al.</i> 1994; Witek <i>et al.</i> 2005
	<i>M. lobicornis</i> Nylander, 1846	Als <i>et al.</i> 2004
<i>M. angulimodis</i> Ruzsky, 1905	Woyciechowski <i>et al.</i> 2006	
<i>M. forcipata</i> Karavaiev, 1931	Woyciechowski <i>et al.</i> 2006	
<i>M. kamtschatica</i> Kupyanskaya, 1986	Woyciechowski <i>et al.</i> 2006	

Table 1. Records of *Phengaris* caterpillars' presence in *Myrmica* colonies (continued).

<i>Phengaris</i> species	Host ant	References
	<i>M. kurokii</i> Forel, 1907	Als <i>et al.</i> 2004
	<i>Aphaenogaster japonica</i> Forel, 1911	Sibatani <i>et al.</i> 1994; Als <i>et al.</i> 2004
<i>P. nausithous</i> (Bergsträsser, 1779)	<i>M. rubra</i> (Linnaeus, 1758)	Thomas <i>et al.</i> 1989; Stankiewicz & Szelezniw 2002; Buszko <i>et al.</i> 2005; Tarrally & Varga 2005a
	<i>M. scabrinodis</i> Nylander, 1846	Munguira & Martín 1999
<i>P. arion</i> (Linnaeus, 1758)	<i>M. sabuleti</i> Meinert, 1860	Malicky 1969; Thomas <i>et al.</i> 1989
	<i>M. rubra</i> (Linnaeus, 1758)	Malicky 1969 (may be misidentification)
	<i>M. scabrinodis</i> Nylander, 1846	Thomas <i>et al.</i> 1989
	<i>M. lobicornis</i> Nylander, 1846	Szelezniw <i>et al.</i> 2002; Szelezniw <i>et al.</i> 2005
<i>P. arionides</i> (Staudinger, 1887)	<i>M. rubra</i> (Linnaeus, 1758)	Fukuda <i>et al.</i> 1992
	<i>A. japonica</i> Forel, 1911	Sibatani <i>et al.</i> 1984
<i>P. atroguttata</i> (Oberthür, 1876)	<i>M. formosae</i> Wheeler, 1929	Als <i>et al.</i> 2004
	<i>M. rugosa arisana</i> Wheeler, 1930	Als <i>et al.</i> 2004
	<i>M. kurokii tipuna</i> Santschi, 1937	Als <i>et al.</i> 2004
<i>P. daiozana</i> (Wileman, 1908)	<i>M. formosae</i> Wheeler, 1929	Als <i>et al.</i> 2004

on one “primary host ant species” of *Myrmica* (Table 2). A more intricate version of this view accepts that some other *Myrmica* species might function as “secondary hosts”, in whose nests the *Phengaris* larvae would survive in a considerably lower rate than at nests of their primary host (Als *et al.* 2004; Thomas *et al.* 2005). Because any *Myrmica* can adopt any *Phengaris* caterpillar, survival within ant nests is a crucial issue here (e.g. Wardlaw *et al.* 1998). All *Phengaris* species survive in nests of many *Myrmica* species in the laboratory (Wardlaw *et al.* 1998), but differences in survival of caterpillars in various *Myrmica* nests appear if the host colonies starve (Elmes *et al.* 2004).

Still later, analyses of cuticular hydrocarbons (Akino *et al.* 1999; Elmes *et al.* 2002) and field observations (Elmes *et al.* 1994, Elmes *et al.* 2002) revealed that the specialization of cuckoo *Phengaris* may vary among localities, so that different populations use different host ants. These discoveries, however, did not change a prevailing view of species-specificity among predatory *Phengaris* species.

Therefore, two hypotheses can be distinguished, the *species*

Table 2. Host specificity of *Phengaris* species according to Thomas *et al.* 1989.

<i>Phengaris</i> species	<i>Myrmica</i> host
<i>P. arion</i>	<i>M. sabuleti</i>
<i>P. teleius</i>	<i>M. scabrinodis</i>
<i>P. nausithous</i>	<i>M. rubra</i>
<i>P. rebeli</i>	<i>M. schencki</i>
<i>P. alcon</i>	<i>M. rubra</i> (northern Europe)
	<i>M. ruginodis</i> (north-central Europe)
	<i>M. scabrinodis</i> (southern Europe)

*specificity hypothesis*, postulating that individual *Phengaris* butterflies use a single species of *Myrmica* ants as hosts, perhaps with some secondary hosts used on rare occasions, and the *local specialization hypothesis*, postulating that individual *Phengaris* populations have evolved to exploit different *Myrmica* species locally. However, multiple new records of *Myrmica* hosts have appeared in recent years, and it is not clear how these records are consistent with the two hypotheses. In this paper, we use published information to subject the hypotheses to critical scrutiny. We collated the published data on individual ant species recorded as hosts of *Phengaris*, and used them to test the following hypotheses: (I) The number of known host ants per species increases with research intensity. (II) The number of known host ants within a butterfly species increases with the number of quantitative reports. (III) Within quantitatively surveyed populations or sites, the frequency of occurrence of *Phengaris* larvae in *Myrmica* nests reflects the relative local abundance of individual *Myrmica* species. A positive answer to (I) would cast a serious doubt on the entire view of *Phengaris* host specificity, and a positive answer to (II) would also not be consistent with the species specificity hypothesis, whereas a positive answer to (III) would not support local specialization.

## METHODS

We reviewed the literature reporting host ants used by individual *Phengaris* species. For information reported in review articles, we attempted to track original sources. To overcome the fact that not all adopted larvae survive in each ant species, we accepted only records of fully-grown *Phengaris* larvae, pupae or emerging adults. We considered *P. rebeli* as a separate taxon, although there is strong evidence that it just an ecological form of *P. alcon* (Berezcki 2005; Als *et al.* 2004; Pech *et al.* 2004; Fric *et al.* 2007; Pecsénye *et al.* 2007). This was done for practical reasons, as most reviewed publications consider the two as separate species.

We then regressed the numbers of known *Myrmica* hosts per *Phengaris* species against *research intensity* in individual butterflies. We measured the research intensity as the number of papers retrieved from the Web of Science database (©ISI) after searching for “(*Maculinea* OR *Glaucopsyche*) AND [species name]” (*Glaucopsyche* Scudder, 1872 is another invalid synonym of *Phengaris*.) A peculiar trait of Web of Science are ‘keywords plus’, assigned using an automatic algorithm to papers not necessarily related to the topic searched. To avoid possible biases, we repeated the regression with exclusion of such papers.

Papers reporting quantitative circumstances of ants’ surveys, herein referred to as *quantitative reports*, were analysed further. Minimum requirements for a quantitative report was the information on how many nests of how many ant species were examined. Ideally, a quantitative report also informed on the relative abundance of individual *Myrmica* species per study site.

We used the quantitative reports to regress, within each *Phengaris* species, the cumulative numbers of ant species examined against the cumulative numbers of ant species detected as hosts. If a quantitative report referred to multiple sites, each site formed a separate data point. Finally, we used  $\chi^2$  tests to compare, within each quantitatively surveyed site, the frequencies of occupied and unoccupied nests across all ant species surveyed.

## RESULTS

A total of 20 ant species were published as hosts of *Phengaris* [*Maculinea*] butterflies (Tables 1 and 5). In decreasing order, the numbers of known host ants of European species are 15 (*P. teleius*), 8 (*P. rebeli*), 5 (*P. alcon*), 4 (*P. arion*) and 2 (*P. nausithous*). Data for non-European species are very scarce. Still, two ant species are known as hosts of *P. arionides* and three of *P. atroguttata*. All the host ants belong to the genus *Myrmica*, except for *Aphaenogaster japonica*. The number of known host ants increases with research intensity, but the relationships fail short of a nominal significance (log-log scale, all papers:  $a = 0.69$ ,  $F_{1,6} = 5.42$ ,  $P = 0.059$ ; papers excluding those having “*Maculinea*” only in key-words plus:  $a = 0.30$ ,  $F_{1,6} = 4.57$ ,  $P = 0.076$ ). *P. teleius* uses a disproportionately high number of ant hosts, whereas *P. nausithous* disproportionately few (Fig. 1).

Only 26 papers met the criteria for quantitative reports, a majority (16) of them referring to *P. alcon*. There was a strong correlation between the cumulative numbers of surveyed ant species and the numbers of ant species detected as *Phengaris* hosts applied to *P. teleius*, *P. alcon* and '*P. rebeli*'. Only a single quantitative report was available for *P. arion*, whereas for *P. nausithous*, four surveys detected just a single host ant (Table 3). The published evidence is hence consistent with a species-specificity of *P. nausithous*, but not the other species.

The assessments of the *local specialization* hypothesis yielded nominally significant  $\chi^2$  tests, supporting the local specialization hypothesis, only in nine out of 26 quantitative surveys (34.6%, Table 4). It did not prevail in any species, nor in the cuckoo taxa *P. alcon* and '*P. rebeli*', for which it was

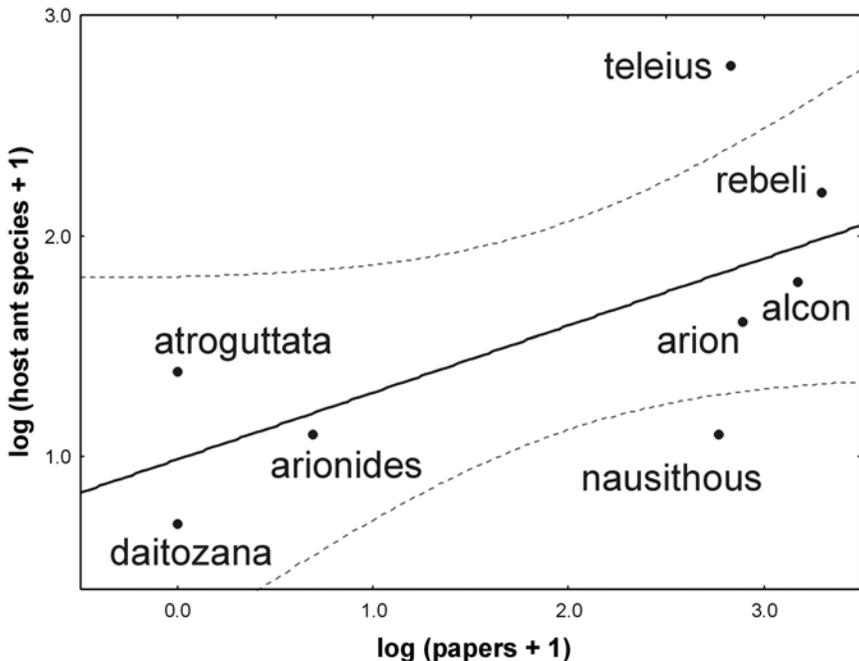


Fig. 1. Relationship between research intensity and number of known host ant species of individual *Phengaris* taxa. Based on Web of Science papers, excluding the papers which contained search terms only in 'Keywords plus'.

Table 3. Cumulative numbers of surveyed ant species and recorded host ant species per individual *Phengaris* taxa.

	<i>P. alcon</i>	<i>P. rebeli</i>	<i>P. teleius</i>	<i>P. nausithous</i>	<i>P. arion</i>
surveyed ant species	8	6	6	5	5
host ant species recorded	5	4	5	1	1

Table 4. Tests of local host ant specificity of the *Phengaris* – *Myrmica* association. Significant results of  $\chi^2$  indicate that the frequency of infested nests deviated from the frequency distribution of individual *Myrmica* species from a local sample.

<i>Phengaris</i> species	Quantitative surveys	Surveys with significant $\chi^2$	Sites with significant $\chi^2$
<i>P. alcon</i>	16	4	Rabjerg Mile, Vejers, Gyttegard, Laeso Ronnerne (all Denmark) (Als <i>et al.</i> 2002)
<i>P. rebeli</i>	3	1	Seredžius (Lithuania) (Stankiewicz <i>et al.</i> 2005)
<i>P. teleius</i>	2	1	Kosyn (Poland) (Stankiewicz & Sielezniew 2002)
<i>P. nausithous</i>	4	2	Kosyn (Poland) (Stankiewicz & Sielezniew 2002) Gödörháza (Hungary) (Tartally & Varga 2005a,b)
<i>P. arion</i>	1	1	Gugny (Poland) (Sielezniew <i>et al.</i> 2003)

first proposed. Testing, across species, if it was supported more frequently in cuckoo or predatory *Phengaris* did not point to any difference, and the results did not depend on whether we treated *P. nausithous* as a cuckoo ( $\chi_1^2 = 0.75$ ,  $P = 0.39$ ) or as a predator ( $\chi_1^2 = 0.95$ ,  $P = 0.33$ ).

## DISCUSSION

Published sources do not support a strict species-to-species *Phengaris* – *Myrmica* relationship. Discoveries of known ant hosts increase with the number of ants surveyed in three European species (*alcon*, ‘*rebeli*’, *teleius*), but not in *P. nausithous*, and no within-species assessment is possible for *P. arion* at this moment. Local-specialization seems to apply only to some populations and the data do not reveal any difference between cuckoos and predators. These observations do not necessarily contradict the association of individual *Phengaris* species with certain species of ants, but they show that it is not consistently supported by data. Before summarizing what actually is supported, we discuss possible sources of biases associated with the origins of the data and with some aspects of *Myrmica* biology.

Table 5. Review of findings of European *Maculinea* butterfly larvae in *Myrmica* ant nests – details

	Country and reference	<i>M. rubra</i>	<i>M. ruginodis</i>	<i>M. scabrinodis</i>	<i>M. vandeli</i>	<i>M. sabuleti</i>	<i>M. salina</i>	<i>M. gallieni</i>	<i>M. schencki</i>	<i>M. lonae</i>	<i>M. sulcinodis</i>	<i>M. spectoides</i>	<i>M. angulimodis</i>	<i>M. fortipava</i>	<i>M. kamtschatica</i>	<i>M. ruginosa</i>	<i>M. lobicornis</i>
<i>P. alcon</i>	Austria (Hörtinger et al. 2003)	+															
	Danmark (Als et al. 2002)	+															
	Spain (Elmes et al. 1994)	+															
	Poland (Sielezniew & Stankiewicz 2004; Stankiewicz et al. 2005a)	+															
<i>P. rebeli</i>	Sweden (Elmes et al. 1994)	+															
	Netherlands (Thomas et al. 1989; Elmes et al. 1994)	+															
	Hungary (Tárrally 2005a; Tárrally & Varga 2005 b)	+															
	Czech Republic (Krenova et al. 2002)	+															
	Hungary (Tárrally 2005a; Tárrally & Varga 2005a, b)	+															
	Austria (Steiner et al. 2003)	+															
	Poland (Steiner et al. 2003; Stankiewicz et al. 2005a)	+															
	Lithuania (Stankiewicz et al. 2005a, b)	+															
	France (Thomas et al. 1989; Steiner et al. 2003)	+															
	Switzerland (Steiner et al. 2003)	+															
<i>P. teleius</i>	Spain (Steiner et al. 2003)																
	Mongolia (Woyciechowski et al. 2006)																
	Hungary (Tárrally 2005b; Tárrally & Varga 2005a)	+															
	Poland (Stankiewicz & Sielezniew 2002; Buszko et al. 2005; Witek et al. 2005)	+															
<i>P. nausithous</i>	France & Poland (Thomas et al. 1989)	+															
	Poland (Buszko et al. 2005; Stankiewicz & Sielezniew 2002)	+															
	Hungary (Tárrally & Varga 2005a)	+															
	France (Thomas et al. 1989)	+															
<i>P. arion</i>	Spain (Mungura & Martín 1999)																
	Poland (Sielezniew et al. 2002, 2005)																
	England, France, Sweden (Thomas et al. 1989)																

(+ - records of presence of caterpillars in *Myrmica* nest)

## Research intensity and publication bias

The measure of research intensity based on reflection of individual *Phengaris* butterflies in scientific literature does not necessarily reflect the intensity of search for novel ant hosts. Some species, such as *P. arion* and '*P. rebeli*', are covered by many modelling and management studies that build on already existing knowledge (e.g. Hochberg *et al.* 1992; Mouquet *et al.* 2005a; Hovestadt *et al.* 2007), whereas for others (most notably *P. teleius*), multiple primary surveys of relationships with ants have been published. On the other hand, an important bias likely shifts the balance towards low specificity. It is well known from all areas of science that negative, confirmatory or just unsurprising results get published less likely than novel or surprising ones (Csada *et al.* 1996; Moller & Jennions 2001). Therefore, surveys just confirming associations with known ant hosts, and hence consistent with the species-specificity hypothesis, may not leave a publication track. On the other hand, whereas findings of novel hosts are likely published even if not based on well-designed surveys, confirmations of already known hosts appear mainly as parts of novel and well-designed studies. It follows that whereas the results opposing the species-specificity hypothesis have a higher chance to get published, reports consistent with the hypothesis have a higher chance to pass our criteria for quantitative surveys, with the two biases likely factoring each other out.

## Caveats of *Myrmica* biology

Surveys of host specificity typically rely on excavating *Myrmica* nests or on trapping emerging adult butterflies. The specificity is then assessed according to the relative representation of infested ant species in local ant assemblage. This approach is complicated by several caveats.

*Specific foraging activity.* The chance that an ant adopts a caterpillar is not related directly to the abundance of ant nests, but to the intensity of ant foraging. This necessarily shifts observed specificity towards more active *Myrmica* species. Individual *Myrmica* may differ greatly in this aspect. Witek *et al.* (2005) reported that the estimates of relative abundance of *M. rubra* based on bait-trapping exceeded by tenfold the estimates based on their nests. Meyer-Hozak (2000) detected only *M. sabuleti* workers using bait traps at

a '*P. rebeli*' site where at least *M. schencki* occurred as well. Nevertheless, the host specificity of the butterfly was always referred to the former ant.

*Seasonal polydomy.* Colonies of many *Myrmica* species frequently occupy several nests during the vegetation season and unite into one nest for the winter period (e.g. Hölldobler & Wilson 1990; Petal 1980). The differences between the spring and autumn nest densities can reach 50% (Petal 1980; Bansbach & Herbers 1999; Herbers & Bansbach 1999) and the rate of polydomy may differ among ants co-occurring within a site (J. Hrcek & P. Pech, unpublished data). Critically, the rate of adoption of *Phengaris* larvae is related to the ant nest densities in late summer, when the adoption occurs, but it is estimated according to nest densities in May/July, when surveys for caterpillars inside ant nests are usually carried out. As a result, the searchers can detect an apparent preference for a more polydomous ant, i.e. the ant with higher ratio of late summer : late spring nests.

*Variation in colony structure.* Demographic parameters of *Myrmica* populations, such as number of queens or fecundity, vary greatly between years and sites even within species (e.g. Elmes & Wardlaw 1982; Elmes & Petal 1990; Wardlaw & Elmes 1996; Elmes *et al.* 1997; Bansbach & Herbers 1999; Maes *et al.* 2003). Whatever the causes of the variation, it must affect the suitability of individual ant species for *Phengaris* (Thomas & Wardlaw 1990).

These caveats may combine so that the specificity observed in the field reflects the activity/abundance of nests at some time before the survey, rather than differential survival in nests of different ant species.

### **Apparent specialization?**

The crucial point little reflected by researchers of the *Phengaris – Myrmica* system is that geographic ranges and habitat niches of individual ant and butterfly species do not necessarily overlap. For example, *M. sabuleti*, considered as the main host of *P. arion*, is absent in Finland, whereas *P. arion* is present there (Kolev 1998). Similarly, the (known) distribution of *M. gallienii* reaches from Western Siberia to Central Europe, whereas the range of *P. teleius* (a parasite of *M. gallienii* in Poland) is much more extended. *M. sulcinodis*, the host of '*P. rebeli*' in Switzerland, is a cold-loving species restricted to high altitudes (with exceptions of the British Isles and Northern Europe). *M. rubra* (host of *P. nausithous*) is extremely restricted in Spain (Czechowski *et al.* 2002);

indeed, caterpillars of Spanish *P. nausithous* parasitize regionally widespread *M. scabrinodis*. By the same token, structurally similar biotopes may be occupied by different ants in different regions, even within a distribution range of a single *Phengaris* species (e.g., ant assemblages of xeric grasslands differ between northern and southern Germany (Seifert 1996) or different areas of Poland (Czechowski *et al.* 2002)).

These observations suggest that the distribution of *Phengaris* may not be primarily driven by association with specific ants, but, as in practically all other butterflies, by such factors as microclimate, sward structure and conditions of host plants. There are multiple supporting indices. *P. teleius* and *P. nausithous* select differently sized host plants, so that conditions favorable for each of the species arise under different mowing or grazing regimes (Figurny & Woyciechowski 1998; Nowicki *et al.* 2005b). The germination of host plants of *P. alcon* and '*P. rebeli*' is facilitated by disturbed sod, and females seem to select plants according to their size, architecture and density (Arnyas *et al.* 2006). The height of sward (grass covered soil) preferred by *P. arion* varies across Europe with climate (Thomas *et al.* 1998; Thomas & Simcox 2005). Repeated failures to document that ovipositing *Phengaris* females orient themselves according to ant presence (Nowicki *et al.* 2005a; Musche *et al.* 2006; Thomas & Elmes 2001) also support the notion that a primary driver in their habitat selection is habitat architecture.

Of course, microclimate and vegetation structure affect the structure of ant assemblages. Instances when only one (or few) ant species exploit the conditions suitable for a *Phengaris* species necessarily manifest as a butterfly-ant specialization. Such cases may explain the locally existent species-to-species relationships, such as that of *P. arion* and *M. sabuleti* in Britain. However, it must be distinguished whether a butterfly is specialised to an ant, or whether we observe an association existing due to other constraints, such as limitations of the ant species pool. Indeed, Thomas *et al.* (1998) noted that *M. sabuleti* was dominant at British *P. arion* sites, as few other *Myrmica* tolerated the short-sward conditions required by the butterfly. In contrast, more *Myrmica* ants occur at continental *P. arion* sites (Czechowski *et al.* 2002; Seifert 1996; Sielezniew *et al.* 2002) although it remains to be shown which ants are actually occupied.

The role of regional species pools cannot be overstated. Many authors claimed or excluded a *Phengaris* specialization with some ant species on the basis of detected ant infestation, regardless of the distribution patterns of other potential *Myrmica* hosts. For example, the reason why caterpillars of *P. alcon* do not infest nests of *M. schencki* is easily interpreted by avoidance by *M. schencki* of wet sites where *alcon*'s host plant, *Gentiana pneumonanthe* Linnaeus, 1753, occurs, rather than by a decreased survival of *P. alcon* brood in *M. schencki* nests.

Additionally, fine-tuned adaptations for single locally or regionally available ant can evolve near geographic ranges of individual butterflies. This might proceed via a relatively a fast reinforcement, particularly in cuckoo species that need to lure ant workers into feeding the butterfly's larvae. Such adaptations may presumably evolve quite rapidly: Als *et al.* (2004) estimated that the incomplete divergence between ecological races of *P. alcon* (i.e., *P. alcon* and '*P. rebeli*') appeared some 0.77 MYA ago and population-level specializations to individual *Myrmica* ants have certainly evolved much faster.

### Specificity revisited

Based on available data, the specificity of individual *Phengaris* species appears as follows.

*P. alcon*, including '*P. rebeli*': A firm evidence for local specialization exists from north-western Europe (*alcon*: Denmark; '*rebeli*': Lithuania), whereas the observations from more southerly areas do not reveal any specialised host ant choice (Elmes *et al.* 2002; Schlick-Steiner *et al.* 2004). The geographic sampling of the two butterflies was sufficiently dense across Europe, allowing the conjecture that specialization tends to develop in isolated areas near their ranges' edges. Considering the recent view that the two butterflies are just ecological forms of one species, the number of ant hosts raises still further.

*P. teleius*: Confirmed from nests of many *Myrmica* species, with no apparent species-specificity. A single case of unequal proportion of larvae in nests of different *Myrmica* was observed by Stankiewicz & Sielezniew (2002). The authors surveyed all *Myrmica* nests at a locality, but noted that colonies of *M. gallieni*, a species that seemed to be avoided, persisted in "very wet places and their nests were sometimes surrounded by water". In these conditions, the lower occurrence of the caterpillars in *M. gallieni* nests is expected.

*P. nausithous*: All existing ant surveys reveal a specific association with *M. rubra*, with an exception from Spain (see above). Woyciechowski *et al.* (2006) attributed this narrow host ant range to restricted distribution of the butterfly, confined to Europe. This narrower ant niche does not seem to correspond with local endangerment, as *P. nausithous* is considerably less threatened than *P. teleius* in parts of their shared range (e.g. Benes *et al.* 2002). The situation in Spain (Munguira & Martín 1999) might represent a case of local specialization near the (southern) species range, similar to the situation observed near the northern range of *P. alcon*.

*P. arion*: Very few surveys of host specificity exist, except for the seminal surveys by Thomas *et al.* (1989) that revealed a strict association with *M. sabuleti* in Western Europe. However, Sielezniew *et al.* (2002) detected an association with *M. lobicornis*, casting a doubt on the strict host ant association of this species.

Asian species: Available data are extremely scarce (cf. Fric & Pech 2006), but nevertheless point to the association of individual butterfly species with multiple ants.

## CONCLUSION

The rapid declines of *Phengaris* species across Europe has inspired a truly massive research effort. This was exemplified by the successful multinational MacMan project, which involved eight institutions from six European nations and a total of about 60 ecologists (Settele *et al.* 2005). The research contributed much to the knowledge of *Phengaris* habitat requirements across the continent (e.g., Settele *et al.* 2005) and to designing appropriate conservation strategies (e.g., Drechsler *et al.* 2006, Johst *et al.* 2006). Despite this progress, the amount of quantitative data on the association of individual *Phengaris* with *Myrmica* ants remains limited. This is to some extent understandable in a case of severely endangered species, in which researchers hesitate to screen multiple locations and regions, as they fear causing unavoidable disturbance to populations.

One point gradually emerging from the research is that it may not be necessary to know precise local associations with ants if we are to conserve *Phengaris* populations and sites. If there are good indices of site quality other than ant presence (e.g., sward height and heterogeneity, quantity and physi-

ological state of host plants), then it is easier to guide management according to those parameters (cf. Maes *et al.* 2004; Wallis DeVries 2004). Indeed, the successful conservation of *P. arion* in Britain, although relying on a detailed understanding of the local butterfly – ant system, manipulates the system via management of vegetation, rather than the ants (Elmes & Thomas 1992; Thomas 1995b). The presence of the ants also rarely limits the presence of *Phengaris*. Practically all *Myrmica* species used as hosts are widespread insects in Europe. From a practical point of view, more naturalists and conservation officers can identify the butterflies and plants than *Myrmica* ants. The precise patterns of the relationship with ants are fascinating, but appropriate conservation measures may be more efficient if based on patterns of vegetation, and abiotic conditions.

We do not call for abandoning research on *Phengaris* – *Myrmica* relationships. We only suggest that it should involve more thorough quantitative sampling across entire geographic and ecological ranges of individual butterflies, including little covered areas of the eastern Palaearctic, and that it should go hand in hand with recording of vegetation structure and microclimate, which may be as decisive for the presence of the butterflies as the composition of local ant assemblages. It is also necessary that researchers clarify, conceptually, what they mean by stating that a *Phengaris* species is ant species-specific. A statement that butterfly X is locally associated with ant Y is factually correct and useful from an applied perspective. Stating that it is specialised to the ant is not supported by data, and may lead to erroneous management prescriptions.

## ACKNOWLEDGMENTS

We would like to thank O. Čížek, K. Fiedler, M. Janda, Z. Křenová, O. Kudrna, H. Malicky, M. Munguira and P. Werner for useful comments and discussions and providing some literature. J. Settele invited us to the Mac-Man project and many ideas in this paper arose in discussions with individual members of the consortium. This work was supported by the Grant Agency of CAS (KJB600070601), Grant Agency of Czech Republic (206/03/H034) and Czech Ministry of Education (FRVS21-2926).

## REFERENCES

- Akino, T., J.J. Knapp, J.A. Thomas & G.W. Elmes 1999. Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. Proceedings of the royal Society of London, Series B, 266: 1419-1426.
- Als, T. D., D. R. Nash & Boomsma J. J. 2002. Geographical variation in host-ant specificity of the parasitic butterfly *Maculinea alcon* in Denmark. Ecological Entomology 27: 403-414.
- Als, T.D., R. Vila, N.P. Kandul, D.R. Nash, S.H. Yen, Y.F. Hsu, A.A. Mignault, J.J. Boomsma & N.E. Pierce 2004. The evolution of alternative parasitic life histories in large blue butterflies. Nature 432: 386-39.
- Arnyas, E., J. Bereczki, A. Toth, K. Pecsénye & Z. Varga 2006. Egg-laying preferences of the xerophilous ecotype of *Maculinea alcon* (Lepidoptera : Lycaenidae) in the Aggtelek National Park. European Journal of Entomology 103: 587-595
- Banschbach, V. S. & J.M. Herbers 1999. Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* [Hymenoptera: Formicidae]. Annals of the Entomological Society 92: 414-423.
- Benes, J., M. Konvicka, J. Dvorak, Z. Fric, Z. Havelda, A. Pavlicko, V. Vrabec & Z. Weidenhoffer (eds) 2002. Butterflies of the Czech Republic: distribution and conservation. SOM, Praha.
- Bereczki, I., K. Pecsénye, L. Peregovits & Z. Varga 2005. Patterns of genetic differentiation in the *Maculinea alcon* species group (Lepidoptera, Lycaenidae) in Central Europe. Journal of Zoological Systematics and Evolutionary Research 43: 157-165.
- Buszko, J., M. Sielezniew, & A.M. Stankiewicz 2005. The distribution and ecology of *Maculinea teleius* and *M. nausithous* in Poland. Pp. 210-213 in Settele J. *et al.* (eds.)
- Chapman, T.A. 1916a. What the larva of *Lycaena arion* does in its last instar. Transactions of the Entomological Society of London 1915: 291-297.
- Chapman, T.A. 1916b. Observations completing an outline of the life history of *Lycaena arion* L. Transactions of the Entomological Society of London 1915: 298-312.
- Csada R.D., P.C. James & R.H.M. Espie 1996. The "file drawer problem" of non-significant results: Does it apply to biological research? Oikos 76: 591-593
- Czechowski, W., A. Radchenko & W. Czechowska 2002. The ants (Hymenoptera: Formicidae) of Poland. Museum and Institute of Zoology Polish Academy of Sciences, Warszawa.
- Drechsler, M., K. Johst, F. Watzold & M.I. Westphal 2006. Integrating economic costs into the analysis of flexible conservation management strategies. Ecological Applications 16: 1959-1966.
- Elmes, G.W. & J. Petal 1990. Queen number as an adaptable trait: evidence from wild populations of two red ant species (genus *Myrmica*). Journal of Animal Ecology 59: 675-690.
- Elmes G.W. & J.A. Thomas 1992. Complexity of species conservation in managed habitats – interaction between *Maculinea* butterflies and their ant hosts. Biodiversity and Conservation 1: 155-169.

- Elmes, G.W. & J.C. Wardlaw 1982. A population study of the ants *Myrmica sabuleti* and *Myrmica scabrinodis* living at two sites in the south of England. I. A comparison of colony populations. *Journal of Animal Ecology* 51: 651-664.
- Elmes, G.W., J.A. Thomas, O. Hammarstedt, M.L. Munguira, J. Martín & J.G. Van der Made 1994. Differences in host-ant specificity between Spanish, Dutch, and Swedish populations of the endangered butterfly, *Maculinea alcon* (Denis et Schiff.) (Lepidoptera). *Memorabilia Zoologica* 48: 55-68.
- Elmes, G.W., J.C. Wardlaw, & B. Barr 1997. Variation in brood-rearing abilities between *Myrmica ruginodis* workers collected from different parts of their range. *Proceedings of the International Colloquia on Social Insects, St. Petersburg*, vol. 3-4: 147-156.
- Elmes, G.W., J.A. Thomas, J.C. Wardlaw, M.E. Hochberg, R.T. Clarke & D.J. Simcox 1998. The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. *Journal of Insects Conservation* 2: 67-78.
- Elmes, G.W., T. Akino, J.A. Thomas, R.T. Clarke & J.J. Knapp 2002. Interspecific differences in cuticular hydrocarbon profiles of *Myrmica* ants are sufficiently consistent to explain host specificity by *Maculinea* large blue butterflies. *Oecologia* 130: 525-535.
- Elmes, G.W., J.C. Wardlaw, K. Schönrogge, J.A. Thomas & R.T. Clarke 2004. Food stress causes differential survival of socially parasitic caterpillars of *Maculinea rebeli* integrated in colonies of host and non-host *Myrmica* ant species. *Entomologia Experimentalis et Applicata* 110: 53-63.
- Fiedler, K. 1989. European and North West African Lycaenidae (Lepidoptera) and their association with ants. *Journal of Research on the Lepidoptera* 28: 239-257.
- Figurny, E. & M. Woyciechowski 1998. Flowerhead selection for oviposition by females of the sympatric butterfly species *Maculinea teleius* and *M. nausithous* (Lepidoptera: Lyceanidae). *Entomologia Generalis* 23: 215-222.
- Fric, Z. & P. Pech 2006. Palaearctic butterfly ecology model for Oriental species conservation. First South East Asian Lepidoptera Conservation Symposium, Hong Kong.
- Fric, Z., N. Wahlberg, P. Pech & J. Zrzavy 2007. Phylogeny and classification of large blues (*Phengaris-Maculinea* clade): total evidence and species concepts. *Systematic Entomology*, in press.
- Fukuda, H., E. Hama, T.A. Kuzuya, A. Takahashi, M. Takahashi, B. Tanaka, H. Tanaka, M. Wakabayashi & Y. Watanabe 1992. The life histories of butterflies in Japan, vol. III, 2nd edn, Hoikusha Publishing, Osaka.
- Herbers, J.M. & V.S. Banskobach 1999. Plasticity of social organization in forest ant species. *Behavioral Ecology and Sociobiology* 45: 451-465.
- Hochberg, M.E., J.A. Thomas & G.W. Elmes 1992. A modelling study of the population dynamics of a large blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. *Journal of Animal Ecology* 61: 397-409.
- Hölldobler, B. & E.O. Wilson 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

- Höttinger, H., F.M. Steiner & B.C. Schlick-Steiner 2003. The Alcon blue *Maculinea alcon* (Lepidoptera: Lycaenidae) in eastern Austria: status and conservation measures. *Ekology (Bratislava)* 22: 107-118.
- Hovestadt, T. O. Mitesser, G.W. Elmes, J.A. Thomas & M. E. Hochberg 2007. An evolutionarily stable strategy model for the evolution of dimorphic development in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *American Naturalist* 169: 466-480.
- Johst, K., M. Drechsler, J. Thomas & J. Settele 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. *Journal of Applied Ecology* 43: 333-342.
- Kawazoe, A., M. Wakabayashi & T. Shirozu 1979. Coloured illustration of the butterflies of Japan. Hoikusha Publishing, Osaka.
- Kolev, Z. 1998. *Maculinea arion* (L.) in Finland - distribution, state of knowledge and conservation. *Journal of Insects Conservation* 2: 91-93.
- Krenova, Z., M. Janda & P. Pech 2002. Modrásci rodu *Maculinea*: ohrožení motýli se zvlátní ekologií. (*Maculinea* blues: threatened butterflies with fascinating life history). *Živa* 50: 169-171.
- Maes, D., H. van Dyck, W. Vanreusel & J. Cortens 2003. Ant communities (Hymenoptera: Formicidae) of Flemish (north Belgium) wet heathlands, a declining habitat in Europe. *European Journal of Entomology* 100: 545-555.
- Maes, D., W. Vanreusel, W. Talloen & H. Van Dyck 2004. Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). *Biological Conservation* 120: 229-241.
- Malicky, H. 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). *Tijdschrift voor Entomologie* 112: 213-298.
- Meyer-Hozak, C. 2000. Population biology of *Maculinea rebeli* (Lepidoptera: Lycaenidae) on the chalk grasslands of Eastern Westphalia (Germany) and implications for conservation. *Journal of Insects Conservation* 4: 63-72.
- Moller, A.P. & M.D. Jennions 2001. Testing and adjusting for publication bias. *Trends in Ecology & Evolution* 16: 580-586.
- Mouquet, N., Belrose, V., Thomas, J.A., Elmes, G.W., Clarke, R.T. & M.E. Hochberg 2005a. Conserving community modules: A case study of the endangered lycaenid butterfly *Maculinea alcon*. *Ecology* 86: 3160-3173
- Mouquet, N., J.A. Thomas, G.W. Elmes, R.T. Clarke & M.E. Hochberg 2005b. Population dynamics and conservation of a highly specialized predator: A case study of *Maculinea arion*. *Ecological Monographs* 75: 525-542
- Munguira, M.L. & J. Martín 1999. Action plan for the *Maculinea* Butterflies in Europe. *Nature and Environment* 97. Council of Europe Publishing, Strasbourg.
- Musche, M., C. Anton, A. Worgan & J. Settele 2006. No experimental evidence for host ant related oviposition in a parasitic butterfly. *Journal of Insects Behavior* 19: 631-643.

- Nowicki, P., M. Witek, P. Skórka & M. Woyciechowski 2005. Oviposition patterns in the myrmecophilous butterfly *Maculinea alcon* Denis & Schiffermüller (Lepidoptera: Lycaenidae) in relation to characteristics of foodplants and presence of ant hosts. Polish Journal of Ecology 53: 409-417.
- Nowicki, P., M. Witek, P. Skórka, J. Settele & M. Woyciechowski 2005. Population ecology of the endangered butterflies *Maculinea teleius* and *M. nausithous* and the implications for conservation. Population Ecology 47: 193-202.
- Pech, P., Z. Fric, M. Konvicka & J. Zrzavy 2004. Phylogeny of *Maculinea* blues (Lepidoptera: Lycaenidae) based on morphological and ecological characters, and the evolution of parasitic myrmecophily. Cladistics 20: 362-375.
- Pecsenye, K., J. Bereczki, B. Tihanyi, A. Tóth, L. Peregovits & Z. Varga 2007. Genetic differentiation among the *Maculinea* species (Lepidoptera: Lycaenidae) in eastern Central Europe. Biological Journal of the Linnean Society 91: 11-21.
- Petal, J. 1980. Ant populations, their regulation and effect on soil in meadows. Ekologia Polska 28: 297-326.
- Schlick-Steiner, B.C., F. Steiner, H. Höttinger, A. Nikiforov, R. Mistrik, C. Schafellner, P. Baier & E. Christian 2004. A butterfly's chemical key to various ant forts: intersection-odour or aggregate-odour multi-host mimicry? Naturwissenschaften 91: 209-214.
- Seifert, B. 1996. Ameisen: beobachten, bestimmen. Weltbild Verlag GmbH, Augsburg.
- Settele, J., E. Kühn & J. Thomas (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/Moscow.
- Sibatani, A., T. Saigusa, & T. Hirowatari 1994. The genus *Maculinea* van Eecke, 1915 (Lepidoptera, Lycaenidae) from the East Palaearctic Region. Tyo to Ga 44: 157-220.
- Sielezniew, M. & A.M. Stankiewicz 2004. Simultaneous exploitation of *Myrmica vandeli* and *M. scabrinodis* (Hymenoptera: Formicidae) colonies by the endangered myrmecophilous butterfly *Maculinea alcon* (Lepidoptera: Lycaenidae). European Journal of Entomology 101: 693-696.
- Sielezniew, M., A.M. Stankiewicz & C. Bystrovski 2002. First observation of one *Maculinea arion* pupa in *Myrmica lobicornis* nest in Poland. Nota Lepidopterologica 55: 249-250.
- Sielezniew, M., A.M. Stankiewicz, L. Luczaj & A. Górnicki 2003. Występowanie i ekologia modraszka Rebela, *Maculinea rebeli* Hirschke (Lepidoptera: Lycaenidae) w Polsce (On the distribution and ecology of Mountain Alcon Blue, *Maculinea rebeli* Hirschke (Lepidoptera: Lycaenidae) in Poland). Przegląd Zoologiczny 47: 211-220.
- Sielezniew, M., J. Buszko & A.M. Stankiewicz 2005. *Maculinea arion* in Poland: distribution, ecology and conservation prospects. Pp. 231-233 in Settele J. *et al.* (eds.).
- Stankiewicz, A. & M. Sielezniew 2002. Host specificity of *Maculinea teleius* Bgstr. and *M. nausithous* Bgstr. (Lepidoptera: Lycaenidae): the new insight. Annales Zoologici 52: 403-408.

- Stankiewicz, A., M. Sielezniew & J. Buszko 2005a. *Maculinea alcon* and *M. rebeli* in Poland: distribution, habitats, host ant specificity and parasitoids. Pp. 90-93 in Settele J. *et al.* (eds.)
- Stankiewicz, A.M., M. Sielezniew & G. Švitra 2005b. *Myrmica schencki* (Hymenoptera: Formicidae) rears *Maculinea rebeli* (Lepidoptera: Lycaenidae) in Lithuania: new evidence for geographical variation of host-ant specificity of an endangered butterfly. *Myrmecologische Nachrichten* 7: 51-54.
- Steiner, F.M., M. Sielezniew, B.C. Schlick-Steiner, H. Höttinger, A. Stankiewicz & A. Górnicki 2003. Host specificity revisited: New data on *Myrmica* host ants of the lycaenid butterfly *Maculinea rebeli*. *Journal of Insects Conservation* 7: 1-6.
- Tartally, A. 2005a. *Myrmica salina* (Hymenoptera: Formicidae) as a Host of *Maculinea alcon* (Lepidoptera: Lycaenidae). *Sociobiology* 46: 1-5.
- Tartally, A. 2005b. *Neotypus melanocephalus* (Hymenoptera: Ichneumonidae): the first record of a parasitoid wasp attacking *Maculinea teleius* (Lycaenidae). *Nota Lepidopterologica* 28: 21-23.
- Tartally, A. & Z. Varga 2005a. *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. 2005b. Host-ant specificity of *Maculinea* species in Hungary, connections with parasitoids and host plants. Pp. 94-98 in Settele J. *et al.* (eds.).
- Thomas, J.A. 1995a. The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society* 56 (Suppl.): 55-72.
- Thomas, J.A. 1995b. The ecology and conservation of *Maculinea arion* and other European species of large butterfly. *In*: Pullin AS (ed.) *Ecology and conservation of butterflies*. pp. 180-197. Chapman & Hall, London.
- Thomas, J.A. & G.W. Elmes 1998. Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. *Ecological Entomology* 23: 427-464.
- Thomas, J.A. & G.W. Elmes 2001. Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. *Proceedings of the Royal Society of London B* 268: 471-477.
- Thomas, J.A. & D.J. Simcox 2005. Contrasting management requirements of *Maculinea arion* across latitudinal and altitudinal climatic gradients in west Europe. Pp. 240-244 in Settele J. *et al.* (eds.)
- Thomas, J.A. & J.C. Wardlaw 1990. The effect of queen ants on the survival of *Maculinea arion* in *Myrmica* ant nests. *Oecologia* 85: 87-91.

- Thomas J.A., D.J. Simcox, J.C. Wardlaw, G.W. Elmes, M.E. Hochberg & R.T. Clarke 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *Journal of Insect Conservation* 2: 39-46.
- Thomas, J.A., G.W. Elmes, J.C. Wardlaw & M. Woyciechowski 1989. Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* 79: 452-457.
- Thomas, J.A., G.W. Elmes, K. Schönrogge, D.J. Simcox, & J. Settele 2005. Pp. 99-104 in Settele J. *et al.* (eds.).
- VanSwaaay, C.A.M. & M.S. Warren 1999. Red Data Book of European butterflies (Rhopalocera). Nature and Environment, No. 99. Council of Europe Publishing, Strasbourg.
- WallisDeVries, M.F. 2004. A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. *Conservation Biology* 18: 489-499.
- Wardlaw, J.C. & G.W. Elmes 1996. Exceptional colony size in *Myrmica* species (Hymenoptera: Formicidae). *The Entomologist* 115: 191-196.
- Wardlaw, J.C., G.W. Elmes, & J.A. Thomas 1998. Techniques for studying *Maculinea* butterflies: I. Rearing *Maculinea* caterpillars with *Myrmica* ants in the laboratory. *Journal of Insect Conservation* 2: 79-84.
- Web of Science, <http://portal.isiknowledge.com/> (6.1.2007)
- Witek, M., P. Nowicki, P. Skórska, E. Sliwinska & M. Woyciechowski 2005. Host ant specificity and integration rate with *Myrmica* ants in larvae of *Maculinea teleius* butterflies. Pp. 105-106 in Settele J. *et al.* (eds.).
- Woyciechowski, M., J. Slowik & M. Muehlenberg 2006. Hosts of the butterfly, *Maculinea teleius*, among *Myrmica* ants in Northern Mongolia (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae). *Sociobiology* 48: 493-502.
- Wynhoff I. 1998. Lessons from the of reintroduction *Maculinea teleius* and *M. nausithous* in the Netherlands. *Journal of Insect Conservation* 2: 47-57.



