

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

by

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## 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

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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. kamschatkica</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

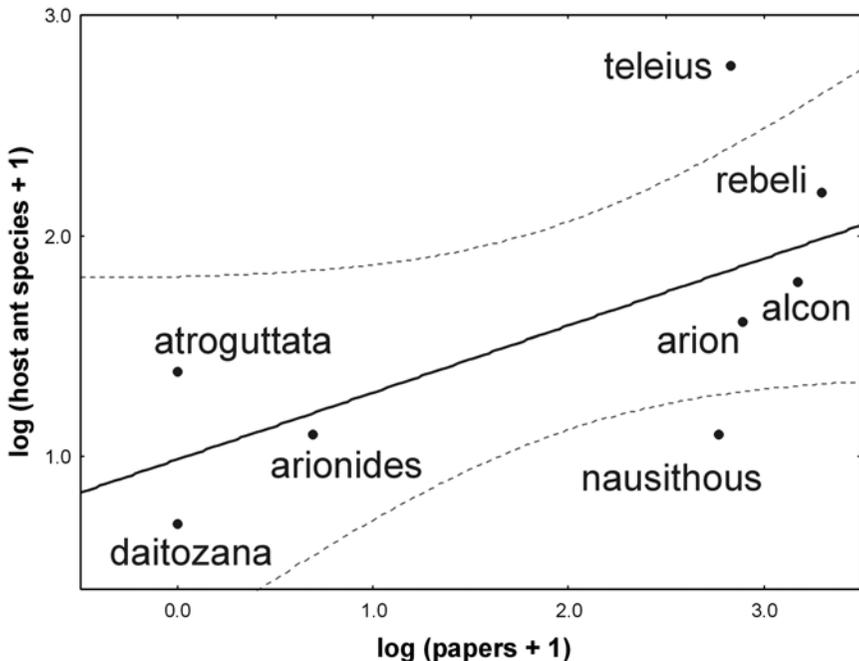


Fig. 1. Relationship between research intensity and number of known host ant species of individual *Phengaris* taxa. Based on Web of Science papers, excluding the papers which contained search terms only in 'Keywords plus'.

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)																
	Sweden (Elmes et al. 1994)	+															
<i>P. rebeli</i>	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)	+															
<i>P. teleius</i>	France (Thomas et al. 1989; Steiner et al. 2003)	+															
	Switzerland (Steiner et al. 2003)																
	Spain (Steiner et al. 2003)																
	Mongolia (Woyciechowski et al. 2006)																
	Hungary (Tárrally 2005b; Tárrally & Varga 2005a)	+															
<i>P. nausithous</i>	Poland (Stankiewicz & Sielezniew 2002; Buszko et al. 2005; Witek et al. 2005)	+															
	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 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.

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