Host ant specificity of large blue butterflies *Phengaris* (Maculinea) (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe

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**Abstract.** Butterflies of the genus *Phengaris* have a highly specialised life cycle involving an obligatory relationship with *Myrmica* ants. A knowledge of the host ant specificity is essential for understanding the relationship between a particular *Phengaris* species and its hosts and also important for the conservation of these butterflies. Data on host ant specificity were collected in Poland, the Czech Republic, Slovakia and Ukraine. Five different *Myrmica* species were used by *P. teleius* as hosts (*M. scabrinodis, M. rubra, M. ruginodis, M. rugulosa* and *M. gallienii*) and at most localities it was not possible to distinguish a primary host – i.e. several *Myrmica* species were parasitized to similar extents. Three populations of *P. nausithous* were found in Poland and Ukraine. In every case, *M. rubra* was its primary host, although in the Kraków region (Poland) two nests of *M. scabrinodis* and two of *M. ruginodis* were infested by this butterfly species. *P. alcon* in the four populations investigated in Poland and Ukraine invariably only used *M. scabrinodis* as a host despite the presence of other *Myrmica* species. These results obtained suggest lack of host specificity in *P. teleius* and high host specificity in *P. nausithous*, which mainly uses *M. rubra* as its host across Europe. Moreover, the three populations of *P. alcon* investigated seem to be highly specific and use *M. scabrinodis* as a host, which confirms the high local specialisation of these populations.

**INTRODUCTION**

Most of the relationships between ants and lycaenid butterflies seem to be mutualistic (Pierce, 1987; Fiedler, 1991, 2001) but in some cases, larvae of certain butterfly species can exploit ant nests as a food resource and shelter and behave as well specialized social parasites (Cottrell, 1984; Maschwitz et al., 1984; Fiedler, 2001).

Probably, the most studied parasitic myrmecophilous relationship is the one between *Phengaris Doherty, 1891* (a junior synonym – *Maculinea* van Eecke, 1915, see Fric et al., 2007) butterflies and *Myrmica Latreille, 1804* ants (Thomas & Settele, 2004). Females of *Phengaris* lay eggs on a specific foodplant and then after about three weeks, young larvae hatch from eggs and feed on the seeds or flowers of the plant. On reaching the fourth instar, the larvae drop to the ground and wait for foraging *Myrmica* ants, which take them to their nests. *Phengaris* caterpillars are parasites of *Myrmica* nests and have evolved different strategies for exploiting *Myrmica* host nests (Thomas & Elmes, 1998). Caterpillars of *Phengaris teleius* Bergsträsser, 1779 and *P. arion* Linnaeus, 1758 prey on ant brood and are called “predatory” species (Thomas et al., 1991; Thomas & Wardlaw, 1992), whereas those of *P. alcon* Denis & Schiffermüller, 1775 and *P. rebeli* Hirschke, 1905 are termed “cuckoo” species, as they mimic ant larvae and are fed directly by workers (Elmes et al., 1991a, b). There is no precise information on the feeding behaviour of *P. nausithous* Bergsträsser, 1779 larvae inside *Myrmica* nests, but this species may have an intermediate strategy (Thomas & Settele, 2004). The cuckoo species are more advanced in their behaviour and chemical mimicry of their host ants compared to the predatory species (Thomas & Elmes 1998; Als et al., 2004). Moreover, the cuckoo-feeding manner is more efficient and as up to 6–7 times more imagos are produced per ant nest compared to the predatory species of *Phengaris* (Thomas & Wardlaw, 1992; Thomas et al., 1993).

Earlier work suggests that each *Phengaris* species has evolved to parasitize a single and different *Myrmica* species (Thomas et al., 1989) with each species adapted to a single “primary host” ant species and only occasionally found with other *Myrmica*, which are regarded as secondary hosts. Thus, *M. scabrinodis* Nylander, 1846 was recorded as the main host ant of *P. teleius*, while *M. rubra* Linnaeus, 1758 of *P. nausithous*, *M. ruginodis* Nylander, 1846 of *P. alcon*, *M. schencki* Emery, 1984 of
The largest number of Myrmica nests was investigated at three sites in Poland (2520 nests). In the Czech Republic, Slovakia and Ukraine, information on particular field studies is presented in Fig. 1 and Appendix 1. The percentage of nests infested with parasites was the lowest compared to the other ant species at those ant nests. Theoretically, F can vary between 0 (no specificity) to ∞ (complete specificity).

RESULTS

P. teleius was the most abundant species found in 292 nests (at 10 localities) belonging to five Myrmica species (Table 1, Appendix 1). The percentage of nests infested by P. teleius ranged from 1.58% at Přelouč (the Czech Republic) to 10.75% in the Kraków region (Poland). Larvae and/or pupae of P. teleius were found mostly in M. scabrinodis and M. rubra nests. M. scabrinodis was present at all localities used as a host by P. teleius at seven of them, whereas M. rubra was present at six localities and used as a host at each of them (Table 1). Other species of Myrmica such as: M. rugulosa, M. gallienni, M. ruginodis were found (Poland: 1 – Kraków, 2 – Sliwa, 3 – Poleski National Park; Czech Republic: 4 – Přelouč, 5 – Poděbrady Kluk; Slovakia: 6 – Stefanova, 7 – Drogonova Dolina; Ukraine: 8 – Lviv Rudno, 9 – Rudniki, 10 – Kireshi, 11 – Novobarovo, 12 – Kosovanka, 13 – Stari Broskvice).

Interestingly, there were three cases of different host ants at close by localities (20–40 km from each other): Novobarovo and Kireshi (Ukraine), Rudniki and Lviv – Rudno (Ukraine) and Stefanova and Drogonova Dolina (Slovakia). Fisher exact tests or Chi square test were calculated separately for each site in order to compare frequencies of occupied and unoccupied nests for all the ant species at these sites. The only significant result was obtained for the Kraków region ($\chi^2 = 12.19$, d.f. = 3, $P = 0.006$). In this intensively sampled region M. scabrinodis was the most abundant Myrmica species but the percentage of parasitism was the lowest compared to the other ant species (Table 1). Additionally, F indexes calculated for 6 populations of P. teleius showed that there was a mixed...
host used in the Kraków region (Poland), Sliwa (Poland) and Rudniki (Ukraine) (Table 1).

*P. nausithous* was mostly associated with *M. rubra* (23 infested nests) and only in the Kraków region were its larvae occasionally found in colonies of *M. scabrinodis* (2 nests) and *M. ruginodis* (2 nests). Larvae and pupae of *P. alcon* were found at four localities and invariably only *M. scabrinodis* (39 nests) was used as a host, even if other *Myrmica* species were abundant (Table 3). For the three populations of *P. alcon* investigated, *F* values show that *M. scabrinodis* is the species’ primary host.

Depending on the locality, the number of larvae/pupae per infested *Myrmica* nest ranged (mean and SE in parentheses) from: 1–8 (2.2 ± 0.281), 1–11 (1.9 ± 0.41), 1–11 (1.61 ± 0.08) for *P. alcon*, *P. nausithous* and *P. teleius*, respectively and differed significantly between species (Kruskal-Wallis, $\chi^2 = 9.06$, d.f. = 2, $P = 0.01$). Post hoc pairwise comparisons among groups (using Bonferroni correction, $P = 0.016$) revealed a significant difference between the number of larvae/pupae of *P. alcon* and *P. teleius* per infested *Myrmica* nest at all the localities (Mann-Whitney U Test, $P = 0.001$).

**DISCUSSION AND CONCLUSIONS**

Thomas et al. (2005) pointed out that the host specificity of social parasites of ants can increase as the results of better penetration of ant society and by interacting with ants in early stages of the life cycle. Thus, *Phergaris* should be species-specific in term of their host ants. However, the most recent data on host ant specificity in *Phergaris* butterflies contradicts this and in a few populations local specialization occurs (Als et al., 2002; Stankiewicz & Sielezniew, 2002; Stankiewicz et al., 2005; Tartally & Varga, 2005; Pech et al., 2007).

Data presented in this paper concern 10 populations of *P. teleius* from different geographical regions of Central Europe. Of the six potential host species present there *P. teleius* larvae used five of them, the exception being *M. sabuleti*. In Kraków, Sliwa and Rudniki, mixed host populations are used. Interestingly, the *F* value (evaluates the strength of host specificity), is lower for *M. scabrinodis* than *M. rubra* and also lower than 1, which indicates lack of specificity for *M. scabrinodis*. These results are surprising, because the previous studies showed that the survival of *P. teleius* larvae reared in *M. scabrinodis* nests is five times greater than in the nests of other *Myrmica* species (Thomas et al., 1989; Thomas & Wardlaw,
1992). Results presented here show that in 70% of the localities investigated, where *M. scabrinodis* and *P. teleius* co-occurred, the former species was used as the host. However, it is important to note that *M. scabrinodis* is the most frequent *Myrmica* species found at *P. teleius* localities and this may account for why it is so frequently used as a host. Moreover, similar data from Asia, where several host ant species were recorded, including *M. angulinodis* Ruzsky, 1905, *M. forcipata* Karavaiev, 1931, *M. kamtschatica* Kupynskaya, 1986, *M. kurokii* Forel, 1907, *M. lobicornis* Nylander, 1846, and *M. ruginodis* suggests multiple host use by *P. teleius* (for a review see Als et al., 2004, Woyciechowski et al., 2006). Furthermore, *Aphaenogaster japonica* Forel, 1911 was found to be parasitized by *P. teleius* in Japan (Yamaguchi, 1988), proving that *Myrmica* is not the only host genus. To sum up, the findings of earlier studies and those presented in this paper confirm the lack of specificity of *P. teleius* and shows that larvae of this butterfly can use almost every *Myrmica* species that co-occur in its habitat.

Larvae and pupae of *P. nausithous* were found in three different populations in Poland, Slovakia and Ukraine, in which *M. rubra* was predominantly used as the host. This confirms the findings of earlier studies (Thomas et al., 1989; Figurny & Tomaszewicz, 1997; Stankiewicz & Sieleziew, 2002; Tartally & Varga, 2005) that *P. nausithous* almost exclusively uses *M. rubra* as its host across Europe. This high specificity is consistent with the finding that *M. rubra* has similar hydrocarbon profile over a wide geographical scale (from West Russia – near Moscow to West Scotland – Hebrides), which indicates that its colonies are chemically very similar across Europe (Elmes et al., 2002). Interestingly, in the Kraków region, we found two nests of *M. scabrinodis* and two *M. ruginodis* with larvae of *P. nausithous*. In this context, it is worth noting, that hydrocarbon profiles of *M. ruginodis* and *M. rubra* are chemically the most similar among the *Myrmica* species investigated by Elmes et al. (2002). The use of *M. scabrinodis* is also previously reported from Spain (Munguira & Martin, 1997) and recently from Romania (Tartally et al., 2008). However, one cannot exclude the possibility that all these exceptions are cases in which *P. nausithous* larvae were initially adopted by a *M. rubra* colony, the nest site of which was subsequently abandoned and taken over by a colony of another species. It is known that switching nest sites is a typical behaviour of *Myrmica* ants (Elmes et al., 1998).

The *F* values calculated for Polish populations of *P. alcon* revealed that *M. scabrinodis* is its primary host ant there. This is not surprising since at each locality all larvae were found exclusively in nests of this *Myrmica*

### Table 2. Host ant use by *P. nausithous*. The number of *Myrmica* nests at each site refers to areas of meadow within 2 m of *S. officinalis*.

| Site                  | Ant species        | Number of nests in site | Number and percentage of nests with *P. nausithous* | Number of larvae/pupae of *P. nausithous* | Specificity (*F*) |
|-----------------------|--------------------|-------------------------|-----------------------------------------------------|------------------------------------------|------------------|
| Kraków (Poland)       | *M. scabrinodis*   | 1585 (68.4%)            | 2 (0.1%)                                             | 3                                         | 0.03             |
|                       | *M. rubra*         | 392 (16.9%)             | 20 (5.1%)                                            | 28                                        | 23.8             |
|                       | *M. ruginodis*     | 299 (12.9%)             | 2 (0.7 %)                                            | 12                                        | 4.4              |
|                       | *M. rugulosa*      | 40 (1.8%)               | –                                                   | –                                         | –                |
| Stari Broskvice (Ukraine) | *M. scabrinodis*   | 18 (78.3%)              | –                                                   | –                                         | –                |
|                       | *M. rubra*         | 5 (21.7%)               | 1 (20%)                                             | 1                                         | –                |
| Dragonova dolina (Slovakia) | *M. scabrinodis*   | 26 (24.5%)              | –                                                   | –                                         | –                |
|                       | *M. rubra*         | 78 (73.6%)              | 2 (2.6%)                                            | 3                                         | ∞                |
|                       | *M. ruginodis*     | 2 (1.9%)                | –                                                   | –                                         | –                |

### Table 3. Host ant use by *P. alcon*. The number of *Myrmica* nests at each site refers to areas of meadow where *G. pneumonathe* (the food plant of *P. alcon*) was present.

| Site                  | Ant species        | Number of nests in site | Number and percentage of nests with *P. alcon* | Number of larvae/pupae of *P. alcon* | Specificity (*F*) |
|-----------------------|--------------------|-------------------------|-------------------------------------------------|-------------------------------------|------------------|
| Kraków (Poland)       | *M. scabrinodis*   | 1116 (68.6%)            | 28 (2.5%)                                        | 63                                   | ∞                |
|                       | *M. rubra*         | 275 (16.9%)             | –                                                | –                                    | –                |
|                       | *M. ruginodis*     | 225 (13.9%)             | –                                                | –                                    | –                |
|                       | *M. rugulosa*      | 10 (0.6%)               | –                                                | –                                    | –                |
| Sliwa (Poland)         | *M. scabrinodis*   | 98 (73.8%)              | 2 (2%)                                           | 3                                    | ∞                |
|                       | *M. rubra*         | 16 (12.0%)              | –                                                | –                                    | –                |
|                       | *M. ruginodis*     | 1 (0.7%)                | –                                                | –                                    | –                |
|                       | *M. gallienii*     | 18 (13.5%)              | –                                                | –                                    | –                |
| Poleski National Park (Poland) | *M. scabrinodis*   | 59 (83.1%)              | 2 (3.4%)                                         | 8                                    | ∞                |
|                       | *M. rubra*         | 8 (11.3%)               | –                                                | –                                    | –                |
|                       | *M. gallienii*     | 4 (5.6%)                | –                                                | –                                    | –                |
| Novobarovo (Ukraine)  | *M. scabrinodis*   | 200 (99.5%)             | 7 (3.5%)                                         | 13                                   | –                |
|                       | *M. ruginodis*     | 1 (0.5%)                | –                                                | –                                    | –                |
species despite the presence of other potential host species such as *M. rubra* and *M. ruginodis* in the Kraków region and *M. rubra* and *M. gallienii* at Sliwa. Similar results for Poland are published by Sielezniew & Stankiewicz (2001). Admittedly, the same authors also discovered two neighbouring populations of *P. alcon* in SE-Poland that simultaneously used *M. scabrinodis* and *M. vandeli* Bondroit, 1920 as host ants, but suspected that *M. vandeli* is a temporary social parasite of *M. scabrinodis* which is almost identical chemically (Radcenko et al., 2003; Sielezniew & Stankiewicz, 2004; Stankiewicz et al., 2005). Pech et al. (2007) pointed out that firm evidence for local specialization of *P. alcon* exists only for a few Danish populations (Als et al., 2002; Nash et al., 2008) while other observations do not reveal any local specificity (Elmes et al., 2002; Schlick-Steiner et al., 2004). In contrast, our data clearly show that in all the Polish populations of *P. alcon* investigated high local specialization occurs.

It is suggested that the cuckoo is more efficient than the predatory strategy (Elmes et al., 1991b) resulting in higher numbers of larvae/pupa produced per *Myrmica* nest. For a few populations of *P. alcon*, *P. nausithous* and *P. teleius* recorded by Thomas & Elmes (1998) the mean number of larvae/pupae per infested nest was 6.0, 2.5 and 1.2, respectively. In this study the corresponding figures are 2.2 for *P. alcon*, 1.9 for *P. nausithous* and 1.6 for *P. teleius*. Hence, even though the general pattern recorded in both studies is very similar, the main difference is in the number of *P. alcon* larvae/pupae per *Myrmica* nest. The sample size is almost the same in both studies (39 vs. 37 nests) but Thomas & Elmes (1998) found quite a few nests with relatively high numbers (>10) of *P. alcon* larvae. A possible reason could simply be a stochastic difference in the spatial overlap in the distribution of *G. pneumonanthe* and ant nests which resulted in more *Phengaris* larvae entering *Myrmica* nests at the sites investigated by Thomas & Elmes (1998). Another possible explanation is that Thomas & Elmes (1998) sampled populations of *P. alcon* that used not only *M. scabrinodis* (as in the present study) but also *M. rubra* and *M. ruginodis*. It is known that *M. rubra* and *M. ruginodis* nests are usually larger than those of *M. scabrinodis* (Wardlaw & Elmes 1996; Radchenko et al., 1997; Skórka et al., 2006) and thus likely support more *Phengaris* larvae.

To summarise, this study confirms the high specificity of *P. nausithous* for *M. rubra* throughout its distribution range and recorded a new host (*M. ruginodis*) for this species. The results also indicate that *P. teleius* does not show either species-specificity or local specialization to host ants. Additionally, our findings clearly show a high local specialization of *P. alcon* populations with *M. scabrinodis* being the primary host. This *Myrica* species is the most common host ant of *P. alcon* in East-central Europe, although other species such as *M. vandeli* or *M. salina* are used occasionally (Sielezniew & Stankiewicz, 2001; Tartally, 2005; Tartally et al., 2008).

Similar to Pech et al. (2007) we think that the regional host species pool is one of the most important factors affecting the host ant specificity of *Phengaris* butterflies, and that stating that a butterfly is specialised to a specific ant at a particular site, if is not supported by data “may lead to erroneous management prescriptions” (Pech et al., 2007, page 15). But, we also argue that insufficient information on host specificity may have the same effect (as was shown for *P. arion* by Thomas 1980, 1995, Thomas et al., 1998). Therefore it is important to further investigate this aspect of the Large Blues’ biology in order to improve management concepts (compare Johst et al., 2006; Drechsler et al., 2007), while in parallel we might be forced to mimic land-use systems as surrogate for the ants’ requirements as long as these are not sufficiently known.

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**APPENDIX 1. Phengaris butterfly and Myrmica ant species composition of the sites investigated (imagoes observed, but no larvae or pupae found).**

| Site name and its number on Fig. 1 | Geographical position | Phengaris species | Myrmica species | Number of nests found |
|-----------------------------------|-----------------------|-------------------|-----------------|----------------------|
| **POLAND**                        |                       |                   |                 |                      |
| Kraków (1)                        | 50°01′N; 19°53′E      | *P. teleius*      | *M. scabrinodis*| 1585                 |
|                                  |                       | *P. nausithous*   | *M. rubra*      | 392                  |
|                                  |                       | *P. alcon*        | *M. ruginodis*  | 299                  |
|                                  |                       |                   | *M. rugulosa*   | 40                   |
| Sliwa (2)                         | 50°35′N; 19°02′E      | *P. teleius*      | *M. scabrinodis*| 98                   |
|                                  |                       | *P. alcon*        | *M. rubra*      | 16                   |
|                                  |                       |                   | *M. ruginodis*  | 1                    |
|                                  |                       |                   | *M. gallienii*  | 18                   |
| Poleski National Park (3)        | 51°21′N; 23°19′E      | *P. alcon*        | *M. scabrinodis*| 59                   |
|                                  |                       | *P. teleius*      | *M. rubra*      | 8                    |
|                                  |                       | *P. arion*        | *M. gallienii*  | 4                    |
| **CZECH REPUBLIC**               |                       |                   |                 |                      |
| Přelouč (4)                       | 50°02′N; 15°34′E      | *P. teleius*      | *M. scabrinodis*| 188                  |
|                                  |                       | *P. nausithous*   | *M. ruginodis*  | 2                    |
| Poděbrady – Kluk (5)             | 50°07′N; 15°08′E      | *P. teleius*      | *M. scabrinodis*| 41                   |
|                                  |                       |                   | *M. sabuleti*   | 26                   |
| **SLOVAKIA**                     |                       |                   |                 |                      |
| Stefanova (6)                     | 48°50′N; 17°27′E      | *P. teleius*      | *M. scabrinodis*| 115                  |
| Dragovna dolina (7)              | 48°46′N; 17°40′E      | *P. teleius*      | *M. scabrinodis*| 26                   |
|                                  |                       | *P. nausithous*   | *M. rubra*      | 78                   |
|                                  |                       |                   | *M. ruginodis*  | 2                    |
| **UKRAINE**                      |                       |                   |                 |                      |
| Novobarovo (11)                  | 48°05′N; 23°30′E      | *P. teleius*      | *M. scabrinodis*| 200                  |
|                                  |                       | *P. alcon*        | *M. ruginodis*  | 1                    |
| Kireshi (10)                      | 48°11′N; 23°21′E      | *P. teleius*      | *M. scabrinodis*| 6                    |
|                                  |                       |                   | *M. rubra*      | 82                   |
|                                  |                       |                   | *M. ruginodis*  | 1                    |
|                                  |                       |                   | *M. gallienii*  | 14                   |
| Rudniki (9)                       | 49°25′N; 23°56′E      | *P. teleius*      | *M. scabrinodis*| 75                   |
|                                  |                       |                   | *M. rubra*      | 17                   |
|                                  |                       |                   | *M. gallienii*  | 14                   |
| Lviv – Rudno (8)                 | 49°51′N; 23°54′E      | *P. teleius*      | *M. scabrinodis*| 66                   |
|                                  |                       |                   | *M. rubra*      | 9                    |
|                                  |                       |                   | *M. ruginodis*  | 30                   |
|                                  |                       |                   | *M. gallienii*  | 1                    |
| Stari Broskivci (13)             | 48°14′N; 25°48′E      | *P. nausithous*   | *M. scabrinodis*| 18                   |
|                                  |                       | *P. teleius*      | *M. rubra*      | 5                    |
| Kosovanka (12)                    | 48°13′N; 25°28′E      | *P. teleius*      | *M. scabrinodis*| 24                   |
|                                  |                       | *P. nausithous*   | *M. rubra*      | 1                    |