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Host ant use by *Phengaris* (= *Maculinea*) *alcon* (Lepidoptera, Lycaenidae) in Poland

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ABSTRACT. *Phengaris alcon* is a socially parasitic butterfly which is endangered or vulnerable in many European countries. Host-ant specificity of the butterfly was studied at nine sites throughout Poland. Except for one locality, we found *P. alcon* full-grown larvae and pupae exclusively in *M. scabrinodis* nests, which confirms that the presence of this ant species is vital for all populations to thrive. Therefore we can exclude with high probability the existence of geographical variation of the specificity of butterfly-ant interactions observed in Western Europe. The infestation rate was 32% and the mean number of *P. alcon* prematures was 3.4. On the site in the Polesie region we found 53 larvae in one colony, but in all other cases we observed up to 10 individuals. *M. vandeli*, which is known as an alternative host for the 'scabrinodis' race of *P. alcon*, was observed only in the Świętokrzyskie region and it was parasitised with a similar rate to the primary host. *M. scabrinodis* was also the most common ant on the site almost everywhere. Only in the Biebrza National Park was the habitat of the butterfly dominated by *M. gallienii*. The very rarely observed event of a nest infested simultaneously by *P. alcon* and *P. teleius* was recorded in the Upper Silesia. Our findings are important for the practical conservation of *P. alcon* in Poland, especially as we noted the deterioration of habitats of the butterfly on a local scale.

KEY WORDS *Phengaris alcon*, *Maculinea, Myrmica scabrinodis*, myrmecophily, social parasitism, Poland.

INTRODUCTION

Myrmecophily is a common phenomena among caterpillars of butterflies belonging to the Lycaenidae family. Most of them show facultative relationships with ants and obligate myrmecophiles are rare among Palearctic lycaenids. In Europe these types of associations were recorded only as far as representatives of two genera are concerned. Larvae of *Plebejus argus* (L.) and *P. idas* (L.) are dependent on the presence of ants and they are involved in mutual relationships with them (FIEDLER 2006). However caterpillars of all members of the genus *Phengaris* Doherty, which, according to FRIC et al. (2007) is a senior synonym of *Maculinea* VAN EECKE, complete their development as social parasites of *Myrmica* LATR. ants.

Phengaris butterflies exploit ant colonies in two ways. *P. arion* (L.), *P. teleius* (BGSTR.) and *P. nausithous* (BGSTR.) prey on ant broods and are regarded as a less advanced species. So-called 'cuckoos' are considered the most advanced myrmecophiles. They are fed by workers with insect prey and regurgitations, like ant larvae (THOMAS & ELMES 1998). This process is enabled by mimicry of ants' chemicals (ELMES et al. 2002, SCHÖNROGGE et al. 2004), and also acoustic signals (BARBERO et al. 2009).

Until recently two 'cuckoo' species were distinguished, i.e. *P. alcon* DEN. et SCHIFF. and *P. rebeli* HIRSCHKE. The taxonomic status of the latter is currently disputed, as recent genetic studies found no differentiation between these two sibling butterflies at species level (ALS et al. 2004, PECSENYE et al. 2007). However due to differences in ecology and some developmental features *P. alcon* and *P. 'rebeli'* should be treated at least as distinct conservation units (SIELEZNIEW & STANKIEWICZ 2007).

As opposed to xerothermophilous *P. 'rebeli'*, *P. alcon* is a rather higrophilous butterfly, inhabiting litter meadows and wet heathlands. It ranges from Southern Spain to Central Asia but shows a scattered pattern of distribution (WYNHOFF 1998). Adults of *P. alcon* are on the wing in July and August. The female oviposits on exposed parts of flowers, buds and upper leaves of *Gentiana pneumonanthe* and, rarely, some other gentians (SIELEZNIEW & STANKIEWICZ 2007). The hatched larva bores into a flower and feeds on developing seeds. After 2-3 weeks at the beginning of the fourth and final instar, the caterpillar leaves the plant. On the ground it can be encountered by a foraging *Myrmica* worker and transported to the nest where it spends next 10 months (or 22 in the case of two year development) and finally pupates (SCHÖNROGGE et al. 2000).

Early studies performed in western Europe suggested that *P. alcon* caterpillars were specialised in the parasitation of *M. ruginodis* (NYL.) (THOMAS et al. 1989). Later the existence of geographical differentiation in the host specificity was revealed. *P. alcon* was detected in the nests of three *Myrmica* species i.e. *M. ruginodis* (the Netherlands), *M. rubra* (L.) (Sweden) and *M. scabrinodis* (NYL.) (Spain) (ELMES et al. 1994). The 'scabrinodis' race is also recorded in France (STOECKEL & MERCIER 2001).

Further studies carried out in different parts of Europe confirmed the existence of local adaptations to parasitation of particular ants but new remarks were also made. In Denmark, on some sites *P. alcon* exploited *M. rubra* and *M. ruginodis* simultaneously, but never *M. scabrinodis* (ALS et al. 2002). It was found that the parasitation rate of *M. rubra* is not even, and positively correlated with chemical similarity between the surface chemistry of the butterfly and its host, which indicates an ongoing co-evolutionary arms race (NASH et al. 2008).

M. scabrinodis proved to be the most commonly used ant in Central and Eastern Europe. For the first time it was identified as a host of *P. alcon* in the region by SIELEZNIEW & STANKIEWICZ (2002) in two localities in Poland (Mazovia and Polesie). Later populations infested simultaneously by *M. scabrinodis* and *M. vandeli* were discovered in the southern part of the country. *M. vandeli* is suspected to be a temporary social parasite of *M. scabrinodis* and these two ants are probably chemically very similar to each other (SIELEZNIEW & STANKIEWICZ 2004). In Hungary, apart from both Polish hosts, *P. alcon* was also locally recorded in colonies of *M. salina* RUZS. but *M. scabrinodis* was by far the most often exploited ant (TARTALLY et al. 2008). Earlier *M. scabrinodis* was reported as a host of the butterfly from eastern Austria (HÖTTINGER et al. 2003). Finally WITEK et al. (2008) found *P. alcon* exclusively with *M. scabrinodis* at three sites in Poland and one site in Ukraine.

The aim of the present paper was to complete information on host ant use of *P. alcon* in Poland. The sites of *P. alcon* are scattered across southern and eastern parts of the country but the species occurs also in isolated localities in the Biebrza Basin and in the Wielkopolska region. It has been found in 35 10 km grid squares so far (STANKIEWICZ et al. 2005) and its national status is assessed as 'vulnerable' (BUSZKO & NOWACKI 2002). Our new data were obtained in all main regions of the distribution of the butterfly in the country including some localities which had not previously been studied.

STUDY SITES AND METHODS

Studies were conducted in the second half of June between 2003 and 2007 on nine sites of *P. alcon* in Poland.

Kuligi (53º38' N/ 22º45' E, 110 m a.s.l.) is the site of the most abundant occurrence of *P. alcon* in the Biebrza National Park (Podlaskie region). The area of occurrence of the butterfly encompasses a dozen or so hectares of litter meadows (some of them mown) and tall herb communities.

Lipa (52º43' N/ 16º46' E, 50 m a.s.l.) is one of a very few isolated and highly vulnerable sites of the butterfly in the Wielkopolska region. The vegetation possessed some characteristics of *Molinion* meadows but it was becoming overgrown with bushes. Just a dozen or so gentians were found.

Augustówka (51°60' N/ 21°29' E, 140 m a.s.l.) is situated in the Mazovia Lowland. The area with *G. pneumonanthe* covered about 1 ha and consisted of two abandoned wet meadows adjacent to mixed forest on one side and a dirt road on the other and separated by a strip of trees. The vegetation could be classified as a mosaic of unfertilised pasture *Nardo-Callunetea* and mainly degenerated *Molinion* meadow. It was becoming overgrown with birches. The first studies at this site were carried out in 2002 (see SIELEZNIEW & STANKIEWICZ 2002).

Serniawy (51°20' N 23°20' E, 170 m a.s.l.) is situated in the Polesie National Park. There were many local populations of *P. alcon* which probably constituted a metapopulation system. We searched a relatively large patch of the habitat with *Molinion* vegetation adjacent to communities of calcareous fens.

Jasiów (51°01' N/ 20°39' E, 350 m a.s.l.) is situated in the Suchedniów-Oblęgorek Landscape Park (Świętokrzyskie region). The site encompassed at least 6 ha of wet meadow surrounded by mixed forests. The vegetation can be described as a mosaic of *Molinion* meadows and tall herb communities with some scattered willows and pines. The lower places were covered with *Carex,* but *G. pneumonanthe* was much more rarely encountered in such places. The first studies at this site were carried out in 2003 (see SIELEZNIEW & STANKIEWICZ 2004).

Kopcie (51°04' N/ 20°39' E, 315 m a.s.l.) is located in the same area as the previous site (4 km away). The type of vegetation was generally similar but a bit lower and more open.

Tyszowce (50°38' N/ 23°45' E, 170 m a.s.l.) is situated in the Hrubieszów Basin (Lublin Upland). The site was a vast mosaic of wet heathlands and *Molinion* meadows where *G. pneumonanthe* is the most often encountered. Occasional burnings were the only form of management.

Hutków (50°34' N/ 23°17' E, 260 m a.s.l.) is situated in the Roztocze region (Lublin Upland) and encompasses a mosaic of strips of mown and abandoned *Molinion* meadows. *G. pneumonanthe* with eggs of *P. alcon* grew the most numerously in unmanaged or extensively used parts of the site.

Wiesiółka (50°25' N/ 19°22' E, 330 m a.s.l.) is situated in the Upper Silesia region. The area of the meadow where the butterfly occurred was about 2 ha, but *G. pneumonathe* was restricted to a smaller patch (ca 0.5 ha), with lower vegetation. The former litter meadow was transforming into a tall herb community as a result of cessation of management. Two other *Phengaris* species were sympatric i.e. *P. teleius* and *P. nausithous.*

We searched for *Myrmica* ants in areas within 2 m of larval food plants on every site. The flowering period of *G. pneumonanthe* usually starts in July, and in June they are not easy to spot. To facilitate this in most cases we marked gentian patches with GPS at the end of the flight period of the butterfly in the season preceding our studies. Therefore our survey was restricted to places where we were able to find either new or dried shoots (often bearing old eggshells of *P. alcon*).

All found nests were very carefully opened and examined for the presence of *P. alcon*. It is known that full-grown larvae are carried by workers to upper chambers during the day and pupation takes place there as well (ALS et al. 2002), therefore there was no necessity for excavation and destruction of colonies. Larvae and pupae were counted and after inspection they were immediately returned to colonies. Then we covered the nests and restored the arrangement of surrounding vegetation as exactly as possible to minimise the impact of our investigation.

Ants were preliminarily identified in the field with hand lenses, but voucher samples of 5-10 workers were collected to confirm this determination in the laboratory according to CZECHOWSKI et al. (2002) and RADCHENKO et al. (2003).

The significance of heterogeneity in the frequency of *P. alcon* presence in nests of different *Myrmica* species on each site was tested, using an extended version of the Fisher exact test, generalised to more than two compared samples (as implemented at http://www.quantitativeskills.com/sisa/).

Fig. 1. Location of sites where host ant specificity of *Phengaris alcon* has been investigated in Poland: ● - the present studies, ○ - SIELEZNIEW & STANKIEWICZ (2002, 2004), □ - WITEK et al. (2008).

RESULTS

A total number of 498 *Myrmica* colonies within 2m of *Gentiana pneumonanthe* plants was investigated at the nine sites of *P. alcon* (Table 1). Five *Myrmica* species were recorded (1-4 species per site) but only *M. scabrinodis* was present on all sites. *M. rubra* was found at Augustówka, Kuligi and Wiesiółka, and *M. ruginodis* at Augustówka, Jasiów and Lipa, whereas *M. gallienii* was observed at Kuligi, Zabieżki and Wojciechów. *M. vandeli* was observed only at Jasiów. *M. scabrinodis* was the most common *Myrmica* ant almost everywhere, with the exception of Kuligi where the turf near gentians was dominated by *M. gallienii* (77%). At Lipa only eight *Myrmica* nests were found and *M. scabrinodis* and *M. ruginodis* were observed in equal proportion.

P. alcon larvae and pupae were found exclusively in nests of *M. scabrinodis* and *M. vandeli* (Table 2). The parasitation rates of *M. scabrinodis* colonies ranged from 22.4% at Kopcie to 50% at Lipa. If data from all sites are grouped together *P. alcon* was present in 31.8% of all examined nests. At Jasiów, 36.8% of *M. vandeli* nests contained larvae and pupae of the butterfly. Significant heterogeneity in host ant use was found at three sites i.e. Augustówka ($p = 0.005$), Jasiów ($p = 0.004$) and Kuligi ($p < 0.001$). Combining the data for all sites, heterogeneity was also highly significant ($p < 0.001$).

A total number of 352 caterpillars and pupae of *P. alcon* were found. From among them 333 individuals were observed in 97 nests of *M. scabrinodis* and 19 individuals in 97 nests of *M. vandeli*. In the case of nests found at Jasiów, two samples of collected workers contained both *M. scabrinodis* and *M. vandeli* individuals. Since the *M. scabrinodis* ones were more numerous in all statistics the mixed colonies were assigned to that species (see also discussion).

The number of *P. alcon* individuals found in a single colony of *M. scabrinodis* varied from 1 to 53. However the highest number, observed at Serniawy, diverged considerably from all other findings (1-10). Our observations indicate that it was an exceptional number and not all caterpillars were able to pupate. In mid July, i.e. the beginning of the flight period of the butterfly, we repeated examination of the infested nest. We counted 50 individuals, among which only three pupated and less than half of the larvae seemed to be fully grown. It was not possible to divide them into two classes of sizes which are typical for growth polymorphism (SCHÖNROGGE et al. 2000).

When data was compiled from all sites, most of the *M. scabrinodis* nests i.e. 61 of 83 (73.5%) hosted only 1-3 larvae (Fig. 2). The mean number of caterpillars per colony ranged from 2.3 at Jasiów to 6.8 at Wojciechów (3.4 per nest at all sites). As far as *M. vandeli* are concerned we observed from 1 to 11 individuals of *P. alcon* in a single colony (2.7 per nest).

At Wiesiółka one nest of *M. scabrinodis* contained a full grown larva and a prepupa of *P. alcon* accompanied by a prepupa of *P. teleius*. Four other individuals of *P. teleius* were also found in one of two colonies of *M. rubra* found near gentians at this site.

Table 1. The number of *Myrmica* colonies found within 2 m of *Gentiana pneumonanthe*, their recorded use by *Phengaris alcon* and a statistical test of host ant specificity at each site: *P* = probability from Fisher exact test that differences in parasitation rates arose by chance.

Site	*Myrmica* species	Number of nests and percentage of all *Myrmica* nests		Number and percentage of nests with *P. alcon*		*P*	Total number of *P. alcon*	Mean number and range of *P. alcon* per infested nest	
Zabieżki	*M. scabrinodis*	113	82.2%	33	29.7%	**0.005**	93	2.8	(1-8)
	M. rubra	17	10.4%	0					
	M. ruginodis	9	3.7%	0					
	M. gallienii	5	3.7%	0					
Jasiów	*M. scabrinodis**	41	53.2%	16	39.0%	**0.004**	36	2.3	(1-9)
	M. vandeli	19	24.7%	7	36.8%		19	2.7	(1-11)
	M. ruginodis	17	22.1%	0					
Kopcie	*M. scabrinodis*	58	100%	13	22.4%	-	40	3.1	(1-9)
Hutków	*M. scabrinodis*	13	100%	6	46.2%	-	21	3.5	(1-9)
Tyszowce	*M. scabrinodis*	9	100%	4	44.4%	-	16	4.0	(1-6)
Serniawy	*M. scabrinodis*	30	83.3%	12	40.0%	0.079	82	6.8	(1-53)
	M. gallienii	6	16.7%	0					
Kuligi	*M. scabrinodis*	24	17.3%	6	25.0%	**<0.001**	28	4.7	(1-10)
	M. gallienii	107	77.0%	0					
	M. rubra	8	5.8%	0					
Wiesiółka	*M. scabrinodis*	13	90.0%	5	38.5%	0.524	11	2.2	(1-3)
	M. rubra	2	10.0%	0					
Lipa	*M. scabrinodis*	4	50%	2	50.0%	0.429	6	3.0	(1-5)
	M. ruginodis	4	50%	0					

* - including mixed colonies of *M. scabrinodis* and *M. vandeli* (see the text for details)

DISCUSSION

The results of the present studies are consistent with other data previously gathered in Poland (Sielezniew & Stankiewicz 2002, 2004, Witek et al. 2008). However, since we studied populations in all main regions of distribution for the first time, we can with high probability make an assumption that all populations of the higrophilous ecotype of P. alcon in our country are dependent on the presence of *M. scabrinodis*. *M. vandeli,* which is the alternative host, was recorded in only one region.

Table 2. Comparison of field data on host ant use by *Phengaris alcon* gathered by different authors in Eastern Europe. *P* = probability from Fisher exact test that differences in parasitation rates arose by chance.

Country, number of sites and authors	*Myrmica* species	Number of nests and percentage of all *Myrmica* nests		Number and percentage of nests with *P. alcon*		*P*	Total number of *P. alcon* and number of individuals per infested nest	
Poland: 9 (present studies)	*M. scabrinodis*	305	61.1%	97	31.8%	**<0.001**	333	3.4
	M. vandeli	19	3.8%	7	36.8%		19	2.7
	M. rubra	27	6.0%	0				
	M. ruginodis	30	5.4%	0				
	M. gallienii	118	23.6%	0				
Poland: 4 (SIELEZNIEW & STANKIEWICZ 2002, 2004)	*M. scabrinodis*	116	73.0%	38	32.8%	**0.030**	118	3.1
	M. vandeli	24	15.1%	10	41.7%		37	3.7
	M. rubra	5	3.1%	0				
	M. ruginodis	10	6.3%	0				
	M. gallienii	4	2.5%	0				
Poland: 3 Ukraine: 1 (WITEK et al. 2008)	*M. scabrinodis*	1473	72.5%	39	2.6%	**0.001**	87	2.2
	M. rubra	299	14.7%					
	M. ruginodis	227	11.2%					
	M. gallienii	22	1.1%					
	M. rugulosa	10	0.5%					
Hungary: 6 Romania: 2 (TARTALLY et al. 2008)	*M. scabrinodis*	155	68.6%	43	27.7%	**0.010**	359	8.3
	M. vandeli	40	17.7%	4	10.0%		16	4
	M. salina	15	6.6%	6	40.0%		137	22.8
	M. gallienii	12	5.3%					
	M. ruginodis	3	1.3%					
	M. schencki	1	0.4%					

Two of our observations of mixed colonies containing both *M. scabrinodis* and *M. vandeli* workers fit the theory about the temporal parasitism of *M. vandeli* (RADCHENKO et al. 2003). It is possible that *P. alcon* caterpillars were adopted by *M. scabrinodis* colonies, which were simultaneously parasitised by queens of *M. vandeli*.

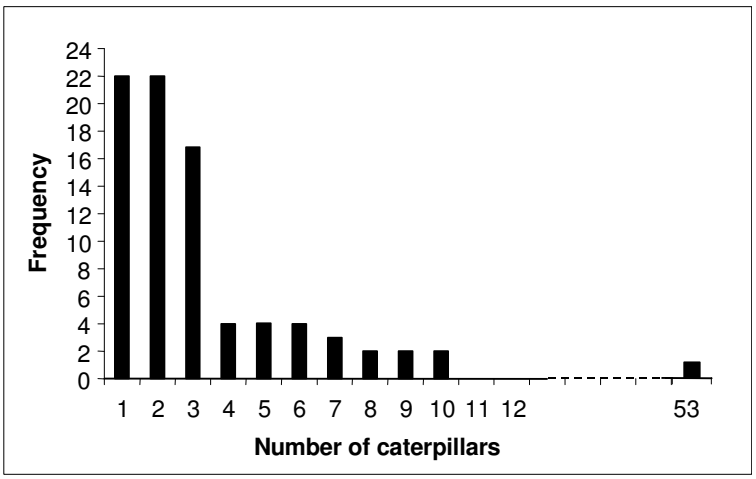

Fig. 2. Frequency distributions of the number of caterpillars of *Phengaris alcon* per infested colony of *Myrmica scabrinodis* (all sites).

It is also plausible that the chemical resemblance of *M. vandeli* and *M. scabrinodis,* enabling the temporal social parasitism of *M. vandeli,* also makes both ants susceptible to infestation by *P. alcon.* However the nature of this phenomenon is still unknown and further studies are required. It is also interesting that the distribution of *M. vandeli* is very restricted compared to its hypothetical host ant. This may be explained by the fact that the niches of both ants (i.e. their preferences for temperature and moisture of soil) overlap only partially (ELMES et al. 1998). In any case *M. vandeli* is presumably a rarer insect species than *P. alcon*.

The existence of geographical variation for *P. 'rebeli'* was only recently discovered in Poland. In the SE part of the country *M. sabuleti* and *M. scabrinodis* were recorded as hosts (SIELEZNIEW & STANKIEWICZ 2007), while in the Pieniny Mts. the butterfly depends exclusively on *M. schencki* (SIELEZNIEW & DZIEKAŃSKA 2008). The same ant species rears *P. 'rebeli'* in Lithuania (STANKIEWICZ et al. 2005). However *P. alcon* shows a uniform pattern of host ant use, and all across Poland, including the most northern and isolated localities like the Biebrza National Park and Wielkopolska, *M. scabrinodis* is the main host ant. Results from Poland along with data from Hungary (TARTALLY et al. 2008) indicate that the '*scabrinodis*' race of *P. alcon* inhabits the whole of Central Europe. Incidentally, *M. scabrinodis* is the only *Myrmica* ant which was recorded as a host of all *Phengaris* species in Europe (PECH et al. 2007).

ALS et al. (2002) suggests that *P. alcon* is adapted to the most common *Myrmica* ant species in habitats where its larval food plant grows. However we found one site (Kuligi)

where *M. scabrinodis* constituted only about a quarter of all *Myrmica* ants present. This may explain the local distribution of the butterfly in the Biebrza National Park, although its larval food plant *G. pneumonanthe* is much more widespread. *M. scabrinodis* is less resistant to flooding and prefers warmer and insolated places, which distinguishes it from the higrophilous *M. gallienii* (CZECHOWSKI et al. 2002). Most of the habitats in the Biebrza National Park are simply too wet for *M. scabrinodis,* and *G. pneumonanthe* seems to be much more tolerant, overlapping both with *M. scabrinodis* and *M. gallienii* niches.

Our studies revealed a high infestation rate of *M. scabrinodis* nests found at the sites i.e. about one third of them host *P. alcon.* This figure is very similar to our previous results but differ considerably from data gathered by WITEK et al. (2008) in Poland and Ukraine, which recorded as great a proportional difference as twelve times fewer infested nests (Table 2). This is presumably related to the methods applied. WITEK et al. (2008) searched for ants in parts of meadows with *G. pneumonanthe,* as they found it 'difficult to detect every plant of this species'. We were much more restrictive in our studies and confined our searching (see also methods) to patches where we found gentians (often also dried shoots from the previous season). We hypothesise that most of the 'empty' nests examined by WITEK et al. (2008) simply could not host *P. alcon* because they were located too far from larval food plants to adopt caterpillars, and the real parasitation rates at their site are underestimated. Therefore it is not surprising that our results are rather similar to the data of TARTALLY et al. (2008) (see Table 2) who applied the same methodology as we did.

We also recorded a higher mean number of *P. alcon* individuals per *M. scabrinodis* (3.4) nest compared to WITEK et al. (2008) (2.2). However our data are strongly influenced by one nest from Serniawy where an unusually high number of larvae and pupae (53) was found. If we omit this result the mean number drops to 2.9. The observed diversity in caterpillar size suggests that the number of butterflies which emerged from that colony in the season was much lower, but this resulted rather from contest competition than the growth dimorphism observed sometimes for *P. alcon* and *P.* '*rebeli*' (SCHÖNROGGE et al. 2000). TARTALLY et al. (2008) did not find evidence for the existence of growth dimorphism in the 'scabrinodis' race of *P. alcon,* either. However they observed a higher mean number of caterpillars per infested colony compared to data from the present studies (Table 2). Possibly it was also influenced by uneven distribution, as they noted as many as 68 caterpillars in one nest, which is probably the highest number of *Phengaris* ever recorded in a *M. scabrinodis* colony. Higher mean numbers of individuals were also reported by THOMAS & ELMES (1998) from Spain. Data concerning other hosts of *P. alcon,* i.e. *M. ruginodis* and *M. rubra* are not comparable because of variation in colony sizes among particular *Myrmica* species (CZECHOWSKI et al. 2002).

Knowledge about host ants is vital for practical conservation of the *Phengaris* butterflies. Our studies showed that isolated regions of occurrence (i.e. Wielkopolska and Biebrza National Park) of the butterfly in Poland, also provide the worst habitat conditions as far as *Myrmica* species composition is concerned. The population at Lipa is probably the most endangered of all studied. Just eight *Myrmica* nests were found and half of them were *M.*

ruginodis, which, in Poland, prefers taller types of vegetation (CZECHOWSKI et al. 2002). Long term abandonment has probably affected the population seriously. Negative changes related to cessation of management were also observed at Augustówka.

During our exploration of *P. alcon* sites we also observed the quick and complete destruction of a population from the Podkarpackie region (Jozefów, 49º40' N/ 21º26' E, 320 m a. s. l.). The whole meadow, which included a patch of *P. alcon* habitat where *G. pneumonathe* grew, was ploughed. Therefore we were not able to finish our studies on host-ant specificity. However *M. scabrinodis* was the most common ant, and observations of caterpillars in their nests in late August suggest that it was also the host of the butterfly there (SIELEZNIEW & STANKIEWICZ-FIEDUREK unpublished). The story of that site shows that inventory works should be followed by action towards the protection of habitats from intensification of land use.

Populations from Polish strongholds of *P. alcon* inhabit meadows, which are at the moment dominated by host ants. However they should be constantly monitored in terms of populations of larval food plants and *Myrmica* ants, to counteract negative changes in time if necessary. Susceptibility to ecological succession depends on the type of vegetation and soil conditions. Most of the *P. alcon* sites were used as extensive pastures in the past, and any conservation measurements should be made very cautiously. Rotational mowing of parts of the habitat in early Autumn is usually recommended as the most appropriate form of management (GRILL et al. 2008), if restoration of light grazing is impossible. Sod cutting should also be locally considered, to enable the germination of *G. pneumonathe* plants, which require patches of bare ground for this process (MOUQUET et al. 2005). The disappearance of larval food plants may be the most significant threat at many sites.

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