Occurrence, development and natural enemies of cecidogenous generations of *Pemphigus gairi* Stroyan (Sternorrhyncha, Pemphigidae)

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ABSTRACT: The paper deals with the occurrence, development and natural enemies of the cecidogenous aphid *Pemphigus gairi* Stroyan (Pemphigidae). The aphid abundantly occurred on leaves of *Populus nigra* and *P. nigra* var. *italica* in Brno in 2003. It was described from England and no information on its occurrence is available in literature from continental Europe. It refers to a holocyclic and heteroecious species. In localities under study, larvae of fundatrices hatched mainly in the last decade of April. Through their sucking on the abaxial face of freshly unfolded leaves of poplars, species-unspecific lengthwise tile-like galls originate on the adaxial face of leaves (near the central leaf vein). During 12 to 14 days, fundatrices mature in galls of an average length and width 11.2 and 3.9 mm, respectively. Adults live about 1.5 months, namely max. until mid-July. They produce on average 75.6 fundatrigeniae which mature to winged migrantes alatae in the course of 16 days. In the period of hatching the first migrants (at the end of May), galls grow up to the final length of about 11.8 mm and width 4.7 mm. In primary slit-shaped caps on the abaxial face of leaves, migrants leave the galls through emergence holes. In a secondary host (*Aethusa cynapium*, Daucaceae), they produce on average about 17.5 larvae of exules. Owing to natural enemies (above all true bugs of the species *Anthocoris minki*), aphids die in 90% of galls.

Keywords: *Pemphigus gairi*; *Populus* spp.; occurrence; development; galls; enemies; *Anthocoris minki*; importance

Aphids (Aphidinea) are a species-rich and numerous and so far relatively little known group of stinging phytophagous insects. They are of a fine petty body and often very complex generation cycles in case of need even with the replacement of host plants. Polymorphism is manifested in the genetically conditioned existence of several morphologically different types of apterous and pterygote females (so-called morphs). This is also the cause of frequently exceptionally difficult determinations of aphids and problems relating the study of their occurrence, biology and harmfulness. Mainly harmful and cecidogenous species are, therefore, best known yet. The species can be usually easily determined according to species-specific galls. Particularly species from a phyllogenetically advanced family Pemphigidae (= Eriosomatidae) are characterized by the formation of true galls (i.e. histologically complicated tumours on plants). In the region of the Czech Republic (CR), this economically important family is represented by 21 genera and 30 species (HOLMAN, PINTERA 1977). As for the species-richest genus *Pemphigus* Htg., in fauna of the CR occur *P. borealis* Tullgr. (Fig. 1), *P. bursarius* (L.) (Fig. 2), *P. gairi* Stroyan (Figs. 3–5), *P. lichtensteini* Tullgr. (= *P. immunis*

Bekt.), *P. populi* Courch. (Fig. 6), *P. populinigrae* (Schr.) (= *P. filaginis* /Bois de Fonsc./) and *P. spyrothecae* Pass. (= *P. spirothecae* Pass.) (Fig. 7). In the CR, *P. phenax* Börn. et Blunck (= *P. dauci* /Gour./), *P. protospirae* Licht., *P. passeki* Börn. and *P. spiriformis* Licht. (= *P. pyriformis* Börn. et Heinze) also probably occur. More than 70 species of the genus have been described in the world, 46 of them form galls on young leaves, petioles and shoots of *Populus* (subgenus *Eupopulus*) (BLACKMAN, EASTOP 1994).

The paper presented deals with the occurrence, development and natural enemies of *Pemphigus gairi* Stroyan which occurred abundantly in *Populus nigra* L. and *P. nigra* L. var. *italica* in Brno in 2003. The aphid forms the same leaf galls in poplars as *P. populinigrae*, *P. phenax* and *P. passeki*. Therefore, the aphid was determined according to fundatrices and fundatrigeniae including migrantes alatae. Determination was carried out by Dr. Jaroslav Holman (České Budějovice) and, thus, I cordially thank for the determination.

P. gairi is a holocyclic species, i.e. a species with a complete generation cycle where one bisexual (amphigonic) generation (sexuales) alternates with several parthenoge-

netic generations. It shows a one-year development and during the development migrates from galls on leaves of the primary host (poplar) to roots of a secondary host (*Aethusa cynapium* L.) (Daucaceae). Thus, it refers to a heteroecious species. Its generation cycle is created by the following morphs: fundatrices, fundatrigeniae including migrantes alatae, exules I (II ?), sexuparae and sexuales.

The species *P. gairi* was described by STROYAN (1964) in England. In addition to the species, other 11 species of the genus *Pemphigus* in 3 subgenera occur in Great Britain (FURK, PRIOR 1975). A subgenus *Pemphigus* is represented there by 9 species (*P. borealis*, *P. bursarius*, *P. populinigrae*, *P. gairi*, *P. phenax*, *P. protospirae*, *P. rubiradicis* Theob., *P. saliciradicis* /Börn./ and *P. spyrothecae*). A subgenus *Parathecabius* is represented there by 2 species (*P. lysimachiae* /Börn./ and *P. auriculae* /Murr./) and a subgenus *Pemphiginus* by 1 species (*P. populi*). These authors mention also a key for determining apterous viviparous females and winged fundatrigeniae and sexuparae of all species mentioned above (except *P. borealis* and *P. rubiradicis*). Radicicolous females are (according to them) undistinguishable from *P. phenax* (living on roots of cultural and wild forms of *Daucus carota*) (Daucaceae) and *P. bursarius* (living on roots of various Compositae, mainly *Sonchus* sp., *Lapsana* sp. and *Lactuca sativa* /L./).

P. gairi, *P. phenax* and *P. bursarius* cannot be determined even according to sexuparae but only according to winged fundatrigeniae (= migrantes alatae). *P. bursarius* can be, however, easily determined for practical purposes according to species-specific sac-shaped galls on leaf petioles of *Populus nigra* and *P. nigra* var. *italica*.

According to LECLANT (1998), the occurrence of the following 9 *Pemphigus* species was proved in France: *P. bursarius*, *P. populinigrae*, *P. phenax*, *P. protospirae*, *P. spyrothecae*, *P. lichtensteini*, *P. populi*, *P. threhernei* Foster and *P. vesicarius* Pass. The species *P. gairi* (so far reported only from England) or *P. passeki* (rarely noticed in Central Europe) has not been found in France yet. No literature data on the occurrence of *P. gairi* are also evidently available from other parts of continental Europe. In the Czech Republic, HOLMAN (pers. commun. 2003) found the species in the vicinity of Prague in *Populus* sp. and *Aethusa cynapium*. Unlike relatively well-known and harmful causal agents of petiole galls (i.e. mainly *P. spyrothecae* and *P. bursarius*), however, no detailed findings exist on the occurrence and biology of *P. gairi* from continental Europe.

RHODEN and FOSTER (2002) give information on the occurrence and aggressive behaviour of the special caste of "soldiers" in galls of *P. gairi*, *P. spyrothecae*, *P. bursarius*, *P. phenax* and *P. protospirae*. AOKI and KUROSU

Table 1. Dimensions of a leaf blade and the size of galls of *Pemphigus gairi* on examined leaves of *P. nigra*. Brno, 2003

Date	Locality	Number of galls	Mean length/width of a leaf blade (mm)	Mean area of a leaf blade (cm^2)	Mean length/width of galls (mm)
8 May	Brno-Žabovřesky	13	83.1/58.8	25.2	9.2/3.0
12 May	Brno-Komín	20	68.5/50.0	18.6	8.8/2.6
19 May	Brno-Žabovřesky	20	77.1/56.0	21.8	10.8/4.2
26 May	Brno-Žabovřesky	20	67.7/47.1	19.8	11.8/4.6
2 June	Brno-Žabovřesky	20	67.2/47.2	16.6	12.0/5.2
9 June	Brno-Žabovřesky	20	70.0/52.0	19.1	12.0/4.8
16 June	Brno-Žabovřesky	20	66.5/49.1	17.8	11.2/4.6
23 June	Brno-Žabovřesky	20	73.2/53.0	20.0	11.4/4.6
30 June	Brno-Žabovřesky	20	76.5/56.5	22.7	11.7/4.6
7 July	Brno-Žabovřesky	20	74.7/54.2	20.0	12.2/4.7
10 July	Brno-Žabovřesky	20	78.4/59.3	23.6	13.0/5.0
14 July	Brno-Žabovřesky	20	75.3/57.3	22.3	12.4/4.6
21 July	Brno-Žabovřesky	20	75.7/57.5	22.9	12.2/4.1
28 July	Brno-Žabovřesky	20	61.6/44.4	14.8	11.8/4.0
11 August	Brno-Žabovřesky	20	74.2/50.8	19.6	11.3/4.2
25 August	Brno-Žabovřesky	20	71.0/55.6	21.1	11.7/4.3
8 September	Brno-Žabovřesky	20	75.0/57.9	23.2	11.7/4.3
22 September	Brno-Žabovřesky	20	72.7/55.3	20.5	11.9/4.0
6 October	Brno-Žabovřesky	20	71.1/56.6	21.3	10.6/4.0
20 October	Brno-Žabovřesky	20	74.7/57.8	23.9	11.4/4.0
3 November	Brno-Žabovřesky	20	73.4/57.9	22.0	12.1/4.3
Total (mean)		413	72.6/53.9	20.7	12.0/4.6[*]

[*]from 26 May to 28 July inclusive

(1986) noticed the existence and defensive role of "soldiers" in colonies of monoecious *P. spyrothecae* in galls on *P. nigra* var. *italica* for the first time. Fundatrices of the aphid produce two morphologically different types of larvae, viz. larvae with strong legs and larvae with normal legs. Larvae with strong legs hold the function of defence against predators. The primary defensive function of "soldiers" of *P. spyrothecae* was experimentally corroborated by FOSTER (1990) and FOSTER and RHODEN (1998). According to the authors, the "soldiers" can effectively protect their colonies particularly from invasions of predaceous heteropterans (*Anthocoris nemorum* /L./, *A. minki* Dohrn.) and hover flies (*Episyrphus auricollis* /Meig./ and *Syrphus ribesii* /L./). At least a quarter of aphids produced by fundatrices (JOHNSON et al. 2002) is adapted for the defence of the aphid population in galls.

P. phenax most resembles the species *P. gairi* from the viewpoint of morphology, galls and bionomy. It is known nearly from the whole Europe, e.g. Spain, France, England, Denmark, Germany, the Netherlands, Poland and Sweden. Exules of *P. phenax* cause rather often economically important damages to roots of *Daucus carota*. Its geographical distribution and biology mention e.g. GONZALES-FUNES and SAVAL (1988). Its development and control are dealt with by SZWEJDA (1997, 1999) and KAHRER (1999). Many common features shows *P. gairi* with a widely distributed species *P. populinigrae* as for the formation of galls and development of fundatrices and fundatrigeniae. In Europe, the primary hosts of the species are *Populus nigra* and *P. nigra* var. *italica* and secondary hosts *Filago* spp. and *Gnaphalium* spp. (Compositae). In spite of a negligible economic importance, *P. populinigrae* is often mentioned in entomological, cecidological and forest protection literature (e.g. GUSEV, RIMSKIJ-KORSAKOV 1953; KRAMM 1953; BAUDYŠ 1954; PAŠEK 1954; PFEFFER et al. 1954; GÄBLER 1965; BUHR 1965; STEFFAN 1972; VASILJEV et al. 1975; RUPAJS 1989 etc.). Recently, the occurrence and development of *P. populinigrae* was described e.g. by TIZADO et al. (1992), PERKINS (1997), LECLANT (1998) etc. Considering the problematic and even impossible determination of *P. gairi*, *P. phenax* and *P. populinigrae* according to galls and considerably difficult determination according to larvae and adults, it is very probable that particularly in cecidological papers, galls of *P. gairi* were incorrectly considered to be galls of *P. phenax* or *P. populinigrae*.

MATERIAL AND METHODS

The paper brings original findings on the occurrence, development and natural enemies of *P. gairi* in galls on *P. nigra* and *P. nigra* var. *italica*. It is based on laboratory examination of galls on leaves of middle-aged and older poplars in 5 urban parts of Brno. During the growing season 2003, groups of galls (usually 20) were sampled. The number of galls taken in each of the control terms corresponded to the time demandingness of subsequent laboratory analyses and the amount of available galls in studied localities.

Of 21 main samplings of galls in *P. nigra* carried out in the period from 8 May to 3 November 2003, 20 samplings were performed in Brno-Žabovřesky and 1 in Brno-Komín. In Žabovřesky, poplars were part of the housing estate and park green vegetation and in Komín part of the riparian and accompanying stand along the Svratka river. Owing to the generally slower dying the galls and somewhat later leaf-fall, analyses of galls on *P. nigra* were carried out (as against galls on *P. nigra* var. *italica*) even

Table 2. Dimensions of a leaf blade and the size of galls of *P. gairi* on examined leaves of *P. nigra* var. *italica*. Brno, 2003

Date	Locality	Number of galls	Mean length/width of a leaf blade (mm)	Mean area of a leaf blade (cm²)	Mean length/width of galls (mm)
5 May	Brno-Komín	67	28.4/21.6	2.9	7.4/2.2
8 May	Brno-Obřany	31	44.4/35.0	9.5	9.5/2.9
12 May	Brno-Komín	20	43.0/34.2	8.3	10.8/3.8
13 May	Brno-Královo Pole	12	46.7/42.8	12.8	11.7/3.6
15 May	Brno-Obřany	20	48.9/37.5	10.7	10.7/3.6
19 May	Brno-Žabovřesky	20	42.5/36.4	9.6	10.8/4.2
29 May	Brno-Obřany	20	39.4/33.4	8.3	12.4/4.7
5 June	Brno-Obřany	20	46.2/41.3	11.4	12.0/5.2
12 June	Brno-Obřany	20	47.3/40.8	11.2	11.7/5.3
19 June	Brno-Komín	20	43.3/33.2	8.6	11.2/4.2
26 June	Brno-Jundrov	20	56.6/45.2	12.6	10.5/4.4
26 June	Brno-Obřany	20	58.2/45.7	14.3	12.7/5.4
3 July	Brno-Obřany	20	50.6/39.5	11.7	11.8/4.3
17 July	Brno-Jundrov	20	53.2/45.7	13.5	11.5/4.3
Total (mean)		330	47.6/40.0*	10.9*	11.7/4.7**

*from 8 May to 17 July inclusive
**from 29 May to 17 July inclusive

Fig. 1. A gall of *Pemphigus borealis* Tullgr. on a young shoot of *Populus nigra* var. *italica*. Bílovice nad Svitavou (former district of Brno-venkov), 3 July 2001

Fig. 2. A gall of *P. bursarius* (L.) on the leaf blade of *P. nigra* var. *italica*. Brno-Královo Pole, 28 May 2003

later than 3 month after their leaving by last individuals of migrantes alatae. From *P. nigra* var. *italica,* galls were taken only in the period from 5 May to 17 July 2003. In total, 14 main samplings were carried out on the tree, viz. 7-times in Brno-Obřany, 3-times in Brno-Komín, twice in Brno-Jundrov, once in Brno-Královo Pole and once in Brno-Žabovřesky. In Obřany, poplars were part of a riparian and accompanying stand of the Svitava river (in Komín and Jundrov, part of stands of the Svratka river), in Královo Pole and Žabovřesky, part of the housing estate and street green vegetation. Due to the small number of available galls and their earlier dying, gall samplings from the poplar were finished soon after the emergence of aphids. In addition to main inspections (Tables 1 and 2), also partial inspections were carried out in the period of the development of aphids in galls according to needs.

In each of the leaves with galls of *P. gairi*, at first length and width of a leaf blade were measured in the laboratory and its area was determined using planimetry. Further, the position of galls on leaves was recorded. The length and width of galls were measured using a microscope. On lengthwise cuts through galls, the gall wall thickness was measured in some galls at their base and top as well as the thickness of a respective leaf by means of micrometry. Based on the comparison of gall dimensions and particular growth stages (instars) of aphids with an intact development, the proportion was determined of particular instars of fundatrices (and the total proportion of fundatrigeniae) in the increase of gall dimensions.

Attention was paid to the development and health conditions of aphids in galls of *P. gairi*. Using micrometry, length and width of the body of fundatrices were measured

and according to the number of exuviae in galls their instar was derived. By the microscopic dissection of imago ovaries of fundatrices the number of embryos with developed eyes was determined and their length and width were measured. In each of the galls, the number was recorded of fundatrigeniae of particular instars including migrantes alatae. In all fundatrigeniae, the width of crania and body dimensions (length and width) were measured. The instar of fundatrigeniae was determined based on metric (or also morphological) criteria. By means of the microscopic dissection of ovaries of migrantes alatae, the number and size of embryos were determined (i.e. future exules). The aim of the study was to determine the time of the development of particular instars and adults of fundatrices and fundatrigeniae and to find out the physiological and ecological natality of imagoes. The fecundity of fundatrices and migrantes alatae was evaluated in relation to the size of the female body and in relation to the size of galls.

In unopened galls with the intact development of aphids, the number was determined of globular droplet-shaped excrements produced by fundatrices and their diameter was also measured by means of micrometry. Basic information was obtained on the amount of excrements produced by particular instars and adults of fundatrices. The production of excrements was also provisionally determined in galls with fundatrigeniae which were unopened so far. In the period of opening the galls and migrantes alatae flight, it was necessary to finish the study due to removing "honeydew" from galls.

Considerable efforts were exerted to study factors participating in the mortality of *P. gairi* in galls. The role was evaluated of natural enemies in relation to the size of

Fig. 3. A gall of *P. gairi* Stroyan at the base of a the leaf blade of *P. nigra* var. *italica*. Brno-Obřany, 8 May 2003

Fig. 4. A gall of *P. gairi* in the basal third of the leaf blade of *P. nigra* var. *italica*. Brno-Obřany, 8 May 2003

galls. Other factors were also taken into consideration. The galls serve for the factors either as an additional source of food (e.g. caterpillars of Lepidoptera) or as an occasional place for egg-laying (Cicadellidae) or a suitable shelter (Araneida). Findings have been obtained on the biology of a main predator, viz. the true bug *Anthocoris minki* Dohrn. and on its negligible effect on the size differentiation of galls. Adults of Lepidoptera nurtured from caterpillars eating out galls were determined by Dr. Z. Laštůvka (Brno). Heteroptera were identified by P. Kment (Faculty of Science, Charles University, Prague) and Syrphidae by Dr. P. Láska (Olomouc). I would like to express my great acknowledgement to the specialists for their help.

RESULTS AND DISCUSSION

Host plants

Pemphigus gairi is a holocyclic and heteroecious species. Its primary (main) hosts are *Populus nigra* L. and *P. nigra* L. var. *italica*. Its possible occurrence in other poplar species has not been recorded in the literature. *Aethusa cynapium* L. (Daucaceae) (STROYAN 1964) is a secondary host. It is a 5 to 80 cm tall annual, perennial or biennial herb resembling through its leaves parsley. It abundantly accompanies human settlements at lower locations. It occurs in gardens, on composts, along roads at the edge of fields, on wastelands, stubbles and in lawns, viz. on soils rich in nutrients, moist as well as drying. It is abundant in studied localities with *P. nigra* and *P. nigra* var. *italica*. In the near as well as far vicinity, also cultivated and wild forms of *Daucus carota* occur abundantly. The potential occurrence of *P. gairi* in this host or in another related host has to be examined in the future.

Development of fundatrices

P. gairi winters in the stage of fertilized winter eggs, viz. in fissures of bark and on other protected places on stems and large-diameter branches of poplars. In the period of budbreak (usually in the 2nd half of April or at the beginning of May), larvae of fundatrices hatch from eggs. After the short period of rest, larvae travel into crowns to budbreak. At first, they often feed on partly unfolded buds. Then they pass to the abaxial face of leaves and settle near their central vein. In case of the marked incoincidence of

Fig. 5. A gall of *P. gairi* in the central part of the leaf blade of *P. nigra*. Brno-Žabovřesky, 8 May 2003
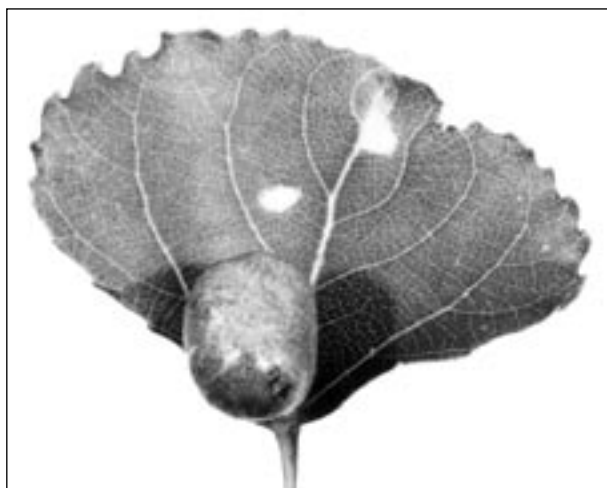
Fig. 6. A gall of *P. populi* Courch. on the leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 28 May 2003

Fig. 7. A gall of *P. spyrothecae* Pass. on the leaf petiole of *P. nigra* var. *italica*. Bílovice nad Svitavou (former district of Brno-venkov), 3 July 2001

the period of budbreak and hatching (for example, during the delayed start of spring and sudden intense warming), larvae starve and mostly die. In studied localities in Brno, larvae of fundatrices hatched in the last decade of April. At the end of April and at the beginning of May, they sucked on intensively growing leaves which obtained their final size as early as at the end of the 1st decade of May (Tables 1 and 2). Based on the tables, it is evident that the area of examined leaf blades of grown up leaves of *P. nigra* as against *P. nigra* var. *italica* was nearly twofold.

Owing to stimulating secretions of salivary glands injected during sucking into quickly growing young tissues the sucked part of a leaf rapidly changes. The leaf tissue along the central vein is stimulated to form a sac-shaped, oval or elliptic diverticulum on the opposite (i.e. adaxial) leaf face (Figs. 3–5). On the abaxial leaf face (close to the hypertrophic central leaf vein), a lengthwise fissure is formed which is of the same length as the gall. The fissure is usually soon quite closed. Inside the soft and relatively thin-wall sac, a spacious cavity is formed with the

environment suitable for the development of a fundatrix and its progeny. Thus, a "true gall" originates which (in contrast to galls of Cynipidae) shows a generally simple morphological structure. In one gall always only one fundatrix develops. Only at the beginning of the period of the development of aphids (up to the occurrence of the 3rd instar), even 2 (maximally 3) larvae of fundatrices can participate in the creation of the only gall. For example, on 8 May 2003, 1 fundatrix occurred in 93.6% of galls with intact development, 2 larvae in 4.8% of galls and 3 larvae in 1.6% of galls. Fig. 8 shows the percentage of galls with the various number of larvae of fundatrices. Owing to competition, weak larvae soon die and so until the stage of imago only 1 larva of fundatrix matures.

Table 3. Length and width of the body of particular instars and imagoes of fundatrices of *P. gairi* in galls on leaves of *P. nigra* and *P. nigra* var. *italica*. Brno, 2003

Instar (stage)	Body length (mm)		Body width (mm)	
	from–to	mean	from–to	mean
1st	0.61–0.78	0.68	0.25–0.32	0.29
2nd	0.71–1.03	0.88	0.36–0.50	0.46
3rd	0.89–1.32	1.10	0.50–0.68	0.58
4th	1.21–1.82	1.41	0.64–1.00	0.78
Imagoes[*]	1.43–1.96	1.73	0.96–1.57	1.16
Imagoes[**]	1.50–2.14	1.85	1.07–1.53	1.31
Imagoes[+]	1.07–2.07	1.57	1.07–1.53	1.27
Imagoes[++]	0.89–1.25	1.06	0.86–1.32	1.06

[*]to the period of the occurrence of fundatrigeniae of the 1st instar inclusive
[**]in the period of the occurrence of fundatrigeniae of the 1st–3rd instars inclusive
[+]in the period of the occurrence of fundatrigeniae of the 1st–4th instars and migrantes alatae inclusive
[++]from the cessation of reproduction to the time of death

Table 4. Maximum length of wax fibres (mm) of larvae and imagoes of fundatrices and fundatrigeniae of *P. gairi* in galls on leaves of *P. nigra* and *P. nigra* var. *italica*. Brno, 2003

Instar (stage)	Fundatrices	Fundatrigeniae
1st	dust	0.36
2nd	0.53	0.46
3rd	0.71	(0.64)
4th	1.00	(0.79)
Imago	1.43	–

The development of fundatrices is heavily affected by physiological and biochemical processes in intensively growing tissues of host plants. In the period of growth, storage starch is changed into soluble sugars and young leaves contain also the largest amount of valuable proteins, vitamins and other biopolymers. Therefore, fundatrices rapidly develop and after 4 moults, they mature sexually. Dimensions (length and width) of the body of particular instars and adults of fundatrices are given in Table 3. In localities under investigation, the development of all 4 instars took (from the beginning of sucking of the 1st instar to the time of the occurrence of the first adults of fundatrices) only 12 to 14 days. The first adults of fundatrices occurred on 9 May (Fig. 9). About 2 days after hatching, adults begin to reproduce.

Mature fundatrices of *P. gairi* are 1.5 to 2.1 (on average 1.8) mm long and 1.1 to 1.6 (on average 1.3) mm wide. Their body is light-yellow-green to light-green. Their dorsal side is covered with fine wax fibres resembling whitish cotton wool. Near the abdomen end, the fibres are usually longest (as many as 1.4 mm long) (Table 4). Flocculi of rather long white fibres occur also in larvae of the 2nd to 4th instars of fundatrices. Only larvae of the 1st instar show fine white waxy powdering above and at the end of their body instead of fibres.

Fundatrices produce spherical colourless droplet-like excrements during sucking which accumulate on the bottom of galls (usually at a slit-shaped cap). Droplets of excrements are covered immediately after elimination by
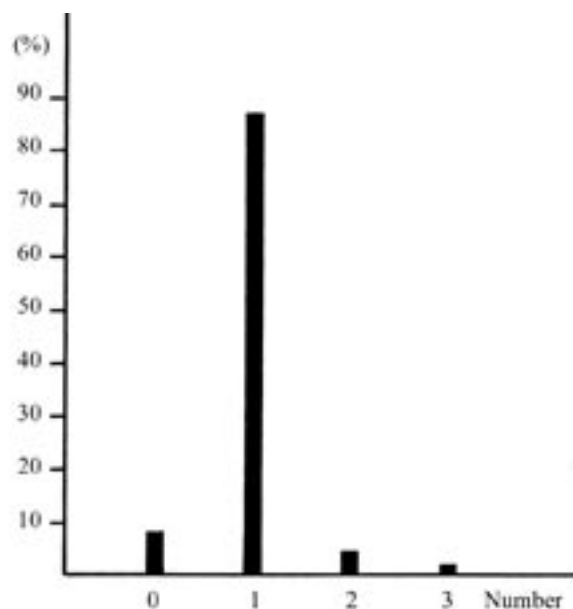

Fig. 8. The percentage of galls of *P. gairi* with a various number of fundatrices on *P. nigra* var. *italica*. Brno-Komín, 8 May 2003

a thin layer of wax powder produced by numerous wax glands. The wax powder thoroughly isolates the droplets from inner walls of galls and thus protects aphids from staining. Until the beginning of reproduction, excrements of fundatrices fill only very small part of the inner space of galls. The excrements help to keep suitable microclimate in galls (particularly air humidity) and together with wax secretions of aphids partly protect from natural enemies. An increase in the number and size of droplets in galls with particular instars and adults of fundatrices shows Table 5.

Adults of fundatrices occurred in studied localities till mid-July, i.e. for the period of 9 weeks. The majority of females with intact development lived 1.5 (max. 2) months. Within this relatively long period, females took food and produced larvae (fundatrigeniae). Dimensions (length and

Table 5. Increase in the number and size of droplets of excrements during the development of the 1st and 2nd generations of *P. gairi* in galls on leaves of *P. nigra* and *P. nigra* var. *italica*. Brno, 2003

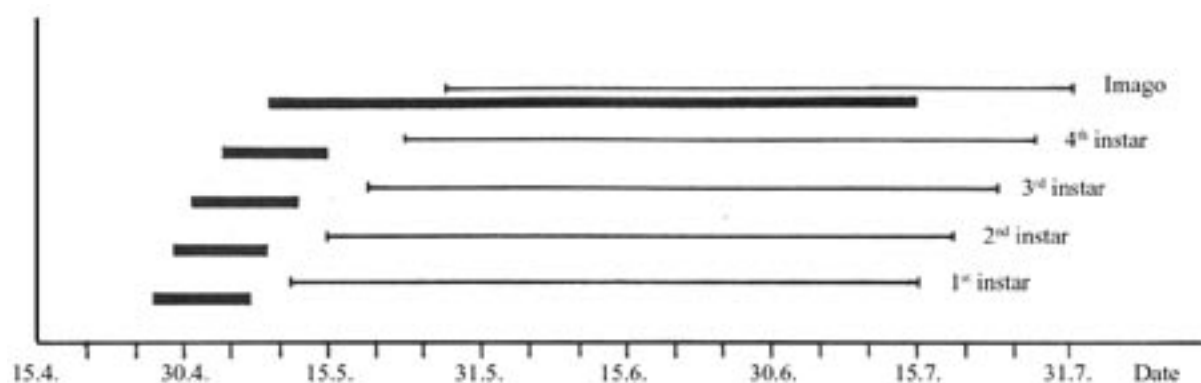| Generation	Instar (stage)	Number of droplets		Diameter of droplets (mm)	
		from–to	diameter	from–to	diameter
	1st	–	–	–	–
	2nd	1–2	1.5	0.14–0.21	0.18
Fundatrices	3rd	1–5	3	0.14–0.46	0.25
	4th	2–12	6	0.14–0.64	0.32
	imago	7–45	25	0.14–0.71	0.36
	1st	30–200	85	0.14–0.89	?
	2nd	50–250	150	0.11–1.10	?
Fundatrigeniae	3rd	20–400	300	0.11–1.43	?
	4th	1–800	(600)	0.11–2.14	?
	imago	?	?	?	?

Fig. 9. A basic scheme of the development of fundatrices (bold) and fundatrigeniae (thin) of *P. gairi*. Brno, 2003
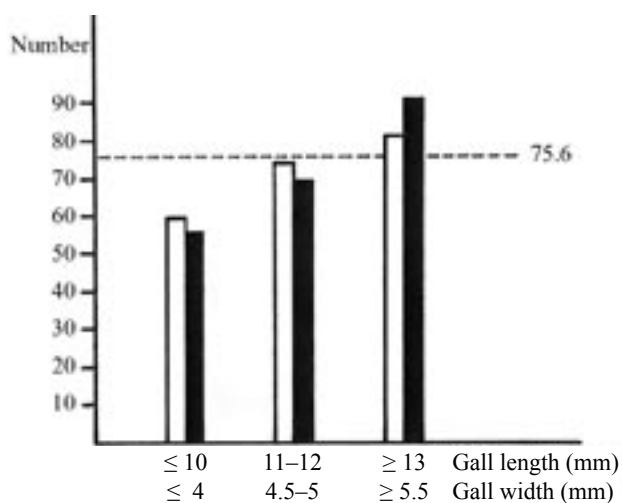

Fig. 10. Physiological natality of fundatrices of *P. gairi* in galls of various length (light columns) and width (dark columns). Average physiological natality is depicted by a dash line. Brno, 26 May to 12 June 2003 inclusive

width) of the imago body of fundatrices culminated in the period of the occurrence of fundatrigeniae of the 1st to the 3rd instar. From the time, their body gradually markedly shortened and partly also became slim (Table 3). Changes in the imago size of fundatrices during their reproduction are undoubtedly related to the number of growing and full-grown embryos of larvae in ovaries. Embryos in the ovaries of adults of fundatrices grow up gradually in the course of sucking being also gradually produced. At the beginning of the period of reproduction (i.e. roughly in mid-May), some 8 to 38 (on average 15) embryos with eyes occurred in ovaries, in half of the period of reproduction (i.e. about at the beginning of June), 17 to 81 (on average 30) embryos with eyes. Later, the number of embryos with eyes gradually decreases and in the 1st half of July, the process of reproduction of fundatrices is finished. Fundatrices produced the greatest number of offsprings from 20 May to 20 June. Embryos with eyes are yellow-green to green, 0.4 to 0.67 (on average 0.55) mm long and 0.2 to 0.27 (on average 0.25) mm wide.

Table 6. The number of embryos (with eyes) in ovaries of fundatrices and the number of fundatrigeniae in galls of *P. gairi* on leaves of a) *P. nigra*, b) *P. nigra* var. *italica*. On 9 and 12 June, the data were affected by the beginning of leaving the galls by migrantes alatae. Brno, 2003

	Date	Locality	Average number of			(%)	
			embryos	born offsprings	total	embryos	born offsprings
a	12 May	Komín	15.0	2.0	17.0	88.2	11.8
	19 May	Žabovřesky	27.1	28.1	55.2	49.2	50.8
	26 May	Žabovřesky	29.4	51.8	81.2	36.2	63.8
	2 June	Žabovřesky	18.0	78.1	96.1	18.7	81.3
	9 June	Žabovřesky	(5.5)	(40.0)	(45.5)	(12.1)	(89.7)
b	12 May	Komín	15.5	4.6	20.1	77.2	22.8
	13 May	Královo Pole	24.9	18.5	43.4	57.3	42.7
	15 May	Obřany	16.4	9.5	25.9	63.4	36.6
	19 May	Žabovřesky	20.8	21.4	42.2	49.2	50.8
	29 May	Obřany	23.7	52.8	76.5	31.0	69.0
	5 June	Obřany	12.0	71.1	83.1	14.5	85.5
	12 June	Obřany	(9.3)	(50.7)	(60.0)	(15.6)	(84.4)

Table 7. The number of embryos (with eyes) in ovaries of fundatrices incl. the number of fundatrigeniae of *P. gairi* in galls in relation to the body length and width of fundatrices: a) at the beginning of the period of reproduction (until the occurrence of the 1st instar of fundatrigeniae incl.), b) in the middle of the period of reproduction (from the occurrence of the 2nd to the occurrence of the 3rd instar of fundatrigeniae incl.), c) at the end of the period of reproduction (from the occurrence of the 4th instar of fundatrigeniae to the occurrence of migrantes alatae incl.) (1 division = 0.0357 mm). Brno, 2003

	Length of fundatrices (divisions)	Mean number of embryos (with eyes) incl. offsprings	Width of fundatrices (divisions)	Mean number of embryos (with eyes) incl. offsprings
a	≤ 45	16.3	≤ 30	18.1
	46–50	20.8	31–35	24.9
	≥ 51	27.9	≥ 36	28.8
	Mean	21.6	Mean	21.6
b	≤ 48	39.0	≤ 33	42.3
	49–53	48.7	34–38	47.5
	≥ 54	49.8	≥ 39	52.6
	Mean	47.7	Mean	47.7
c	≤ 39	54.8	≤ 33	51.4
	40–44	72.2	34–38	88.3
	≥ 45	89.2	≥ 39	93.4
	Mean	76.9	Mean	76.9

Physiological fecundity of fundatrices is relatively high (from 32 to 157 [on average 75.6] larvae). In galls on leaves of *P. nigra*, average physiological fecundity was somewhat (on average by 5 larvae) higher than in galls on *P. nigra* var. *italica*. Fundatrices in larger galls were substantially more fecund than in smaller galls (Fig. 10). In galls with intact development, fundatrices produce 74 to 100% (on average 94.2%) larvae created in ovaries. It means that the ecological fecundity of fundatrices approaches physiological fecundity. In galls under study, the first completely laid fundatrices were found as early as 2 June. After the cessation of reproduction, they die within 1 to 5 days. Wrinkled (diminished) bodies of dead fundatrices remain in galls for a certain time. In the period of growing up and maturing of fundatrigeniae, galls open gradually and fundatrigeniae remove dead fundatrices together with excrements (so-called honeydew) from the galls. Owing to the enormous mortality of fundatrices and fundatrigeniae (caused mainly by *Anthocoris minki*), it was not possible to evaluate exactly the natality of fundatrices from mid-June (Table 6). However, it has been definitely proved that natality significantly increases not only with the size of galls (Fig. 10) but also with the size of fundatrices (Table 7).

Development of fundatrigeniae

In consequence of the long period of reproduction of fundatrices, fundatrigeniae occurred in galls in studied localities from 11 May to 31 July. In the course of about 16-day development, they hatched 4-times and the first migrantes alatae occurred in galls as early as 27 May (Figs. 11 and 12). The first abandoned galls were noticed at the end of June and last migrantes alatae at the end of July. From the end of May to mid-July, all instars of fun-

datrigeniae including migrantes alatae occurred in galls together with fundatrices (Fig. 9).

In contrast to fundatrices, particular instars of fundatrigeniae (with the exception of migrantes alatae) can be distinguished quite reliably according to the cranium width (Table 8). As against fundatrices, the head of fundatrigeniae is more distinct being not retractable into their prothorax and thus, it is also easily measurable. Table 8
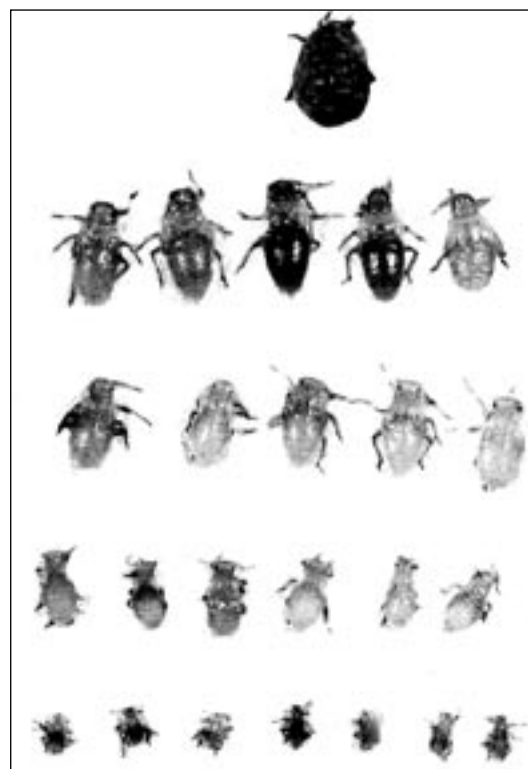

Fig. 11. Imagoes of a fundatrix and fundatrigeniae of the 1st to 4th instars of *P. gairi*

Table 8. The cranium width and the body length and width of fundatrigeniae incl. migrantes alatae *P. gairi* in galls on leaves of *P. nigra* and *P. nigra* var. *italica*. In total 2,128 individuals were measured. Brno, 2003

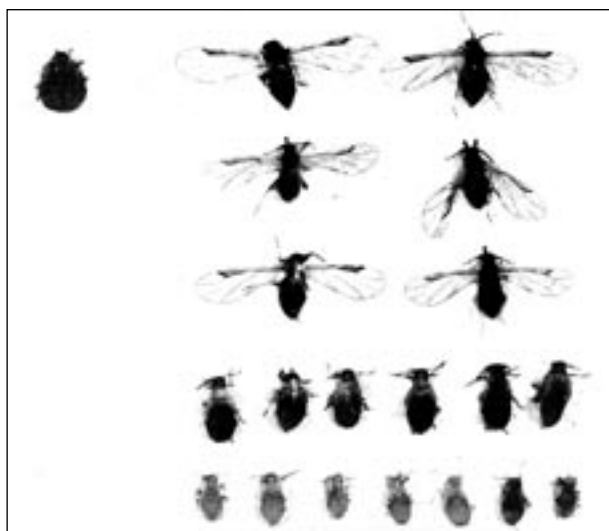| Instar (stage)	Cranium width (mm)		Body length (mm)		Body width (mm)	
	from–to	mean	from–to	mean	from–to	mean
1st	0.18–0.21	0.20	0.61–0.89	0.72	0.25–0.39	0.32
2nd	0.23–0.27	0.25	0.82–1.18	0.98	0.36–0.54	0.44
3rd	0.28–0.34	0.31	1.00–1.53	1.22	0.46–0.71	0.57
4th	0.33–0.39	0.36	1.25–2.14	1.66	0.61–0.96	0.74
Imago	0.32–0.37	0.35	1.32–2.21	1.81	0.57–0.89	0.73

Fig. 12. Imagoes of a fundatrix, fundatrigeniae of the 3rd and 4th instars and of migrantes alatae of *P. gairi*

gives also data on the body length and width of particular instars of the 2nd generation of *P. gairi*. The head width and body dimensions (in divisions) are depicted in Fig. 13. The table and figure show that the cranium of migrantes alatae is (as against larvae of the 4th instar) on average somewhat narrower. On the other hand, migrantes alatae are (as against larvae of the 4th instar) on average a little longer and narrower (Table 8, Fig. 14). Their length is 1.3 to

2.2 (on average 1.8) mm (according to STROYAN 1964, it is 1.5 to 2.2 mm long).

Living fundatrigeniae of the 1st to the 3rd instar are mainly light-yellow-green. However, larvae of the 4th instar have a green abdomen and meso- and metathorax including wing sheaths are yellowish. Migrantes alatae have a black head, thorax, eyes, antennas, legs and veins on wings and a dark green abdomen. Rudiments of wings and paired ocelli appear only in the 3rd instar of fundatrigeniae. In the 4th instar, the 3rd (i.e. unpaired) very petty eyelet occurs in the front part of its forehead. On the dorsal side of an abdomen (mainly in its back part), white waxy plugs of fine wax cotton wool occur in the 1st to 4th instars. They are a product of well-developed wax-forming glands (Table 4).

Numerous colonies of fundatrigeniae produce large amounts of excrements. These gradually accumulate in galls and at the end of the period of development of fundatrigeniae, they often fill the predominant part of the inner space of galls. Globular droplets often pour together thereby increasing their diameter. At the end of the development of the 2nd generation of aphids, there are 1 to 800 (on average 600) droplets of various diameter (0.11–2.14 mm) in galls with the intact development of aphids (Table 5). With the increasing numbers of aphids and amounts of excrements in galls the number of exuviae also increases. The size of galls increases, however, only unsubstantially (Table 9) in the period of the reproduction of fundatrices. The living space of aphids, therefore, de-
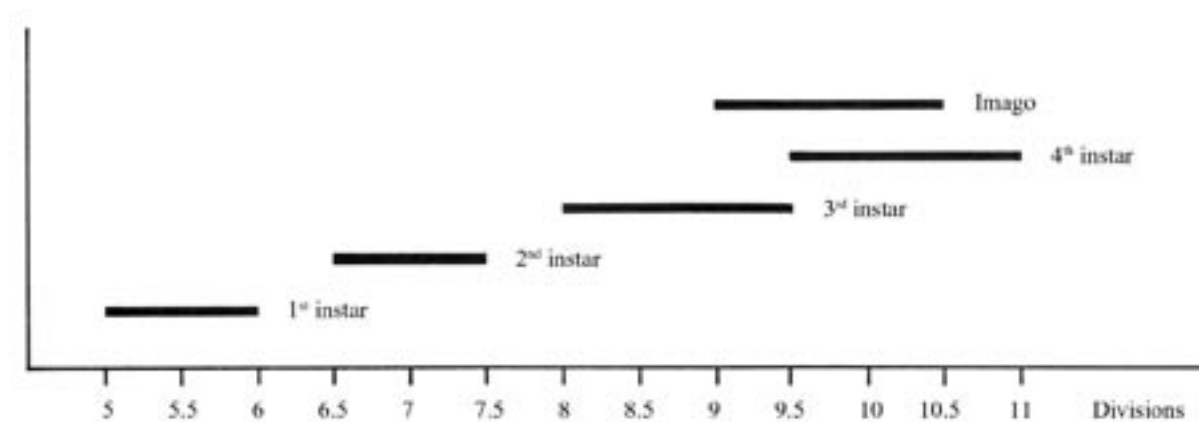

Fig. 13. Width of the cranium of fundatrigeniae of the 1st to 4th instars and of migrantes alatae of *P. gairi* (1 division = 0.0357 mm). Brno, 2003
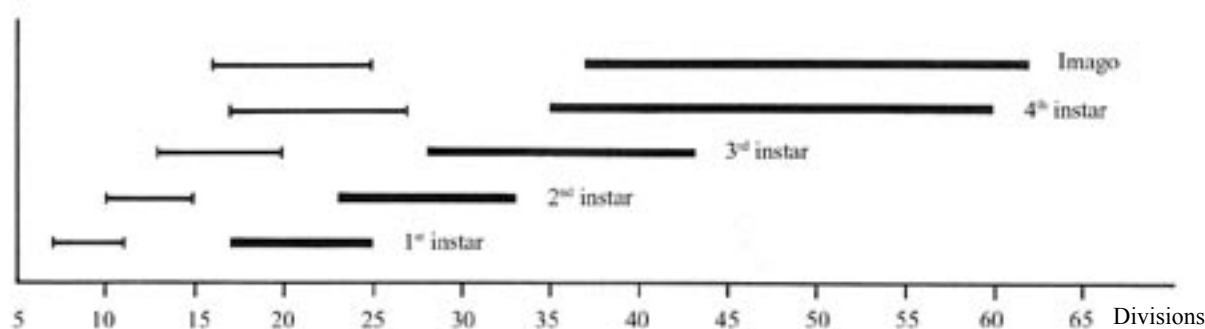
Fig. 14. Length (bold) and width of fundatrigeniae of the 1st to 4th instars and of migrantes alatae of *P. gairi* (thin) (1 division = 0.0357 mm). Brno, 2003

Table 9. Mean dimensions of galls with the intact development of *P. gairi* on leaves of *P. nigra* and *P. nigra* var. *italica* in the period of the occurrence of larvae and imagoes of fundatrices and fundatrigeniae. Brno, 2003

Instar (stage)	Mean length of galls (mm)	Mean width of galls (mm)
1st	5.6	1.7
2nd	7.1	2.1
3rd	9.1	2.7
4th	10.0	3.2
Imagoes*	11.2	3.9
Imagoes**	11.4	4.4
Imagoes***	12.1	4.7

*without fundatrigeniae
**with fundatrigeniae
***with migrantes alatae

creases with the ongoing development of fundatrigeniae. Living conditions of aphids are also quickly deteriorated due to the effect of morphological and physiological changes in ageing tissues of host species.

In the period of hatching the first migrantes alatae (in Brno as early as from 25 May), galls begin to open gradually from below (i.e. in primary slit-shaped caps). At the beginning of June, the majority of galls is open through a narrow fissure or 1 to 3 lengthwise (or even) oval apertures (Table 10). The small part (4.2 to 5.0%) of galls, however, does not open at all until autumn. Usually it refers to galls with prematurely dead fundatrices. Spontaneous opening the galls results in lowering the water content in gall and leaf tissues. Fundatrigeniae obviously participate in en-

larging emergence holes (though minimally only). Small aphids (above all fundatrigeniae of the 1st–3rd instars) often temporarily leave the galls through these holes and appear on leaves near the holes. Aphids use the holes to ventilate the inner space of galls and after reaching their sufficient size also for removing excrements, dead fundatrices and exuviae. Cleaning the galls begins in the period of hatching the first migrantes alatae (i.e. at the end of May) and ends by the emergence of the last imago (i.e. at the end of July – Fig. 9).

Galls of *P. gairi* open usually at the turn of May and June when migrantes alatae account for about 5 to 10% from the total number of fundatrigeniae. Within the period, 40 to 60% of migrants and 40 to 60% of larvae (nymphs) of the last (4th) instar of heteroecious *P. bursarius* are in galls. Also fundatrices of heteroecious *P. populi* begin to reproduce in Brno as early as 18 May. The development of fundatrigeniae including migrantes alatae of *P. bursarius* and *P. populi* goes on very quickly and more or less spontaneously and so in mid-June, the majority of galls is completely abandoned. On the other hand, fundatrices in galls of the monoecious *P. spyrothecae* mature as late as at the end of May and the first fundatrigeniae appear 31 May, however, more frequently at the beginning of June. In this species, offsprings of fundatrices mature sexually into apterous viviparous females as late as the 2nd half of July and August. These females produce about 10 offsprings of the 3rd generation of aphids which develop into winged sexuparae. The sexuparae occur in galls from the beginning of August and mainly at the end of August and in September (URBAN 2002).

Winged forms of *P. gairi* in galls probably take no food and after several days sexually mature in galls. Even mi-

Table 10. Ways of opening the galls of *P. gairi* on leaves of *P. nigra* (in % from the total number of galls analyzed in the given month). Brno-Žabovřesky, 2003

Galls	June	July	August	September	October	November
With a narrow lengthwise fissure	44.8	40.9	40.0	36.4	33.3	32.0
With 1 to 3 lengthwise to oval holes	51.7	54.5	55.0	63.6	62.5	64.0
Unopened	3.5	4.6	5.0	–	4.2	4.0
Total	100.0	100.0	100.0	100.0	100.0	100.0

Table 11. Number of embryos in individuals of migrantes alatae of *P. gairi* in relation to the body length and width (1 division = 0.0357 mm). Brno, 2003

Length of the body of migrantes alatae (divisions)	Mean number of embryos	Width of the body of migrantes alatae (divisions)	Mean number of embryos
≤ 45	13.2	≤ 17	12.9
46–50	16.6	18–19	16.9
51–55	19.6	20–21	17.2
≥ 56	21.9	≥ 22	20.4
Total (mean)	17.5	Total (mean)	17.5

grantes alatae *P. bursarius* and *P. populinigrae* do not take food and, therefore, their mortality in galls treated using contact insecticides is much smaller than mortality of apterous forms of aphids (KRAMM 1953). Through the microscopic dissection of 300 individuals of migrantes alatae *P. gairi* it was found that their ovaries contain 10 to 30 (on average 17.5) larvae of the 1st instar (Fig. 15). The average number of larvae significantly increases with the length and width of the female body (Table 11). The largest females show (as against the smallest females) much greater (even threefold) natality.

Larvae in ovaries are yellow-brown, 0.46 to 0.57 (on average 0.50) mm long and 0.18 to 0.28 (on average 0.22) mm wide. Somewhat smaller embryos (on average 0.44 mm long and 0.18 mm wide) are formed already in ovaries of the 4th instar of fundatrigeniae. These embryos are yellow with dark eyes.

In June and July, migrantes alatae fly over to secondary host plants (i.e. *Aethusa cynapium*). In the plants, the winged virgines produce parthenogenetically larvae of the 1st instar of exules. The larvae travel to roots where they undergo further development under protection of abundant wax fibres. Winged sexuparae (remigrantes alatae) return to primary host plants (i.e. *P. nigra* and *P. nigra* var. *italica*) in October. On the bark of their stems and large branches, the sexuparae produce several larvae. After several moults and not taking food, the larvae mature to apterous males and females of the generation of sexuales.

Sexuales of both sexes show the larva-shaped body and stunted mouth and digestive tract. Fertilized females of the generation lay always only one thick-wall winter egg into bark fissures. Thus, the developmental cycle of *P. gairi* is closed.

Galls

Due to the sucking of fundatrices of *P. gairi* on the abaxial fase of leaves (in the immediate vicinity of the central leaf vein), lengthwise convex tile-like galls are formed on the opposite (i.e. adaxial) face of leaves (Figs. 5–7). The longitudinal slit-shaped opening on the abaxial face of leaves (along the central leaf vein) is usually quite closed during a week-sucking. The second and next instars of fundatrices develop already within rapidly increasing galls. Before the beginning of reproduction of fundatrices, galls reach an average length and width of 11.2 and 3.9 mm, respectively. Due to the further sucking of fundatrices and fundatrigeniae, the average length and width of galls is increased only by 0.6 and 0.8 mm, respectively (Tables 1, 2 and 9).

Full-grown galls with the intact development of aphids are 10 to 16 (on average 11.8) mm long and 4 to 7.5 (on average 4.7) mm wide (and high). The average size of full-grown galls in *P. nigra* is the same as in *P. nigra* var. *italica*. The average length and width (height) of galls on full-grown leaves of both poplars
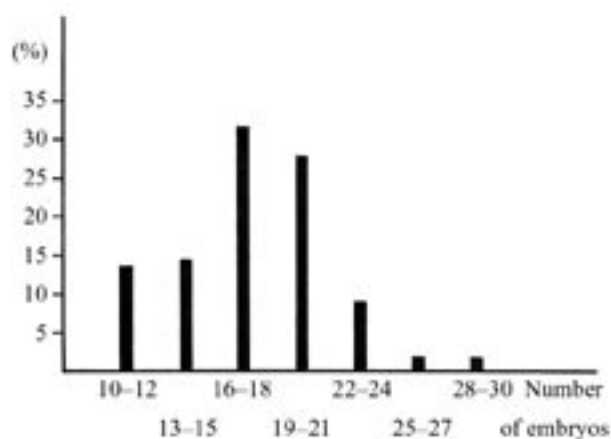
Fig. 15. The percentage of migrantes alatae of *P. gairi* with the various number of embryos in ovaries before the emergence of migrantes from galls. Brno, 2003
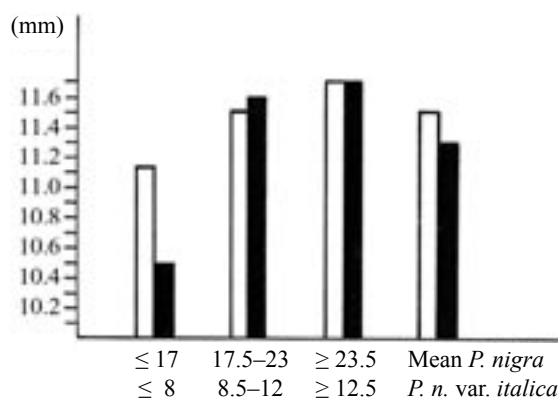
Fig. 16. Length of galls of *P. gairi* on grown-up leaves of *P. nigra* (light) and *P. nigra* var. *italica* (dark) within three area categories of leaves. Brno, 8 May to 11 August 2003 inclusive
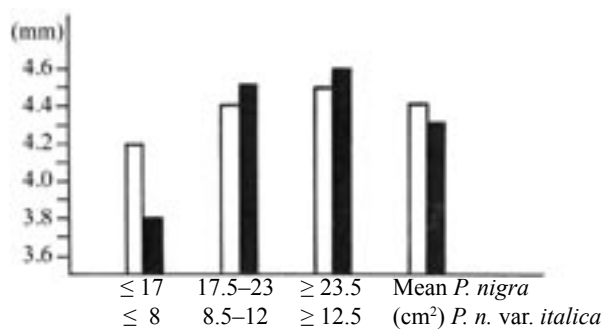
Fig. 17. Width of galls of *P. gairi* on grown-up leaves of *P. nigra* (light) and *P. nigra* var. *italica* (dark) within three area categories of leaves. Brno, 8 May to 11 August 2003 inclusive

significantly increases with the size of a leaf blade (Figs. 16 and 17). It means that galls on large leaves are on average bigger than those on small leaves. Galls of the relative species *P. populinigrae* are 12 to 23 mm long and 7 to 10 mm wide (RUPAJS 1989). According to a preliminary study carried out by PERKINS (1997), galls of *P. populinigrae* are about 14.9 mm long and about 5.8 mm wide (and high).

Galls of *P. gairi* are thin-wall and not-lignifying. Their walls are always thickest at the gall top and thinnest at its base. At the top of galls, walls are 0.53 to 0.75 (on average 0.64) mm thick and at the base 0.28 to 0.46 (on average 0.38) mm in the 1st decade of May. During May and June, the average thickness of gall walls at their top is increased to 1.25 mm and at their base to 0.61 mm. The thickness of undamaged leaf blades amounts to 0.07–0.18 (on average 0.12) mm in the 1st decade of May and in the course of the growing season (in contrast to galls), it does not increase. Near places affected by the sucking of fundatrices, also central leaf veins markedly swell (as against unsucked veins about 1.8-times).

The galls are mostly yellow-green, moderately glossy and smooth on their surface. Part of the galls (in *P. nigra* about 20%, in *P. nigra* var. *italica* about 45%) is slightly reddish. From mid-June, abandoned galls begin gradually

Fig. 19. Two galls of *P. gairi* on a leaf of *P. nigra* var. *italica* (of this, one gall in the basal part of a lateral leaf vein). Brno-Komín, 8 May 2003

to die, brown and blacken. The course of gall death on leaves of *P. nigra* is (as against galls on leaves of *P. nigra* var. *italica*) much slower continuing till the autumnal leaf fall (Fig. 18).

The overwhelming majority of studied galls was localized at the central leaf vein between 2 lateral veins. Only very sporadically (0.1%), galls were situated at lateral leaf veins (Fig. 19). On leaves of *P. nigra*, only one gall occurred in 95.8% (on leaves of *P. nigra* var. *italica* in 97.3%). Some 4.2 and 2.7% of leaves of *P. nigra* and *P. nigra* var. *italica*, respectively, were affected by two galls. Both galls were almost always localized at the central leaf vein, viz. one after another, exceptionally side by side (along both sides of the leaf vein) or at the central vein and lateral vein (Fig. 19). On 1 leaf, more than 2 galls were never found. On leaves of *P. nigra*, the majority of galls (72.2%) occurred in the central third of the leaf blade. On leaves of *P. nigra* var. *italica,* the majority of galls
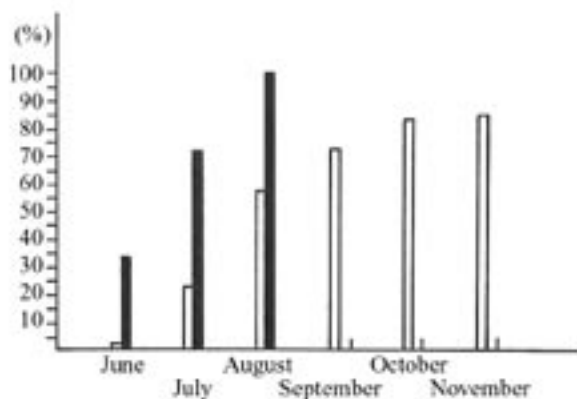

Fig. 18. Increase in the percentage of dying and dead galls of *P. gairi* on *P. nigra* (light) and *P. nigra* var. *italica* (dark). Brno, 2003
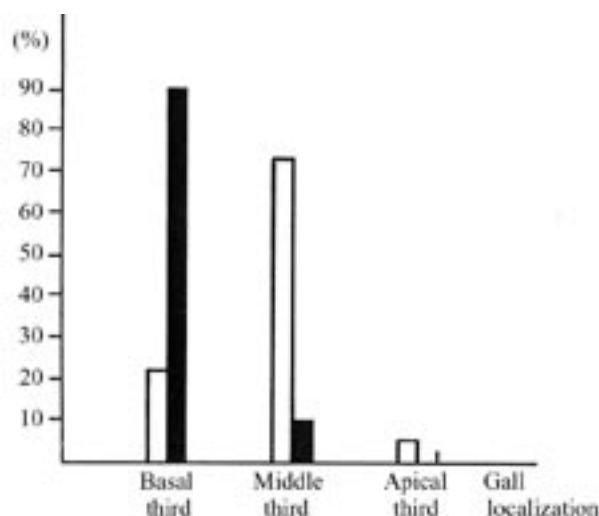

Fig. 20. Localization of galls of *P. gairi* on the leaf blade of *P. nigra* (light) and *P. nigra* var. *italica* (dark). Brno, 2003

Table 12. Results of the analysis of health conditions of *P. gairi* in galls on leaves of *P. nigra*. Brno, 2003

Date	Number of galls	Number/percent of occupied (disturbed) galls									Total
		Anthocoris	Anthocoris + Lepidoptera	Anthocoris + Neuroptera	Anthocoris + Aphidiidae	Lepidoptera	Syrphidae	Aves	unopened	unknown cause	
8 May	13	–	–	–	–	–	–	–	–	–	–
12 May	20	–	–	–	–	–	–	–	–	2/10	2/10
19 May	20	3/15	–	–	–	–	–	1/5	–	1/5	5/25
26 May	22	9/41	–	–	–	1/5	1/4	–	–	1/4	12/54
2 June	20	9/45	–	–	–	3/15	–	1/5	–	1/5	14/70
9 June	20	13/65	1/5	–	–	2/10	–	–	–	–	16/80
16 June	20	17/85	–	–	–	1/5	1/5	–	–	–	19/95
23 June	20	17/85	–	1/5	–	–	–	–	–	1/5	19/95
30 June	20	14/70	1/5	–	–	2/10	–	1/5	1/5	–	19/95
7 July	20	10/50	2/10	–	–	5/25	–	–	–	–	17/85
10 July	20	15/75	2/10	–	–	2/10	–	–	–	–	19/95
14 July	20	12/60	1/5	1/5	–	2/10	–	–	1/5	–	17/85
21 July	20	9/45	1/5	–	–	6/30	–	1/5	–	–	17/85
28 July	20	10/50	2/10	3/15	–	3/15	–	–	–	1/5	19/95
11 Aug.	20	9/45	5/25	1/5	–	2/10	–	1/5	–	–	18/90
25 Aug.	20	6/30	5/25	1/5	1/5	5/25	–	1/5	–	–	19/95
8 Sep.	20	6/30	6/30	–	1/5	4/20	1/5	–	–	–	18/90
22 Sep.	20	7/35	4/20	2/10	1/5	4/20	–	–	–	–	18/90
6 Oct.	20	9/45	2/10	1/5	1/5	4/20	–	–	–	1/5	18/90
20 Oct.	20	3/15	7/35	–	1/5	5/25	1/5	–	–	1/5	18/90
3 Nov.	20	5/25	5/25	1/5	1/5	5/25	–	–	1/5	–	18/90
Total (mean)*	120	11.7/58.3	1.5/7.5	0.7/3.3	–	3.3/16.7	–	0.3/1.7	0.3/1.7	0.2/0.8	18.0/90.0

*from 30 June to 28 July inclusive

Table 13. Results of the analysis of health conditions of *P. gairi* in galls on leaves of *P. nigra* var. *italica*. Brno, 2003

Date	Number of galls	Number/percent of occupied (disturbed) galls									Total
		Anthocoris	Anthocoris + Lepidoptera	Neuroptera	Aphidiidae	Lepidoptera	Syrphidae	Aves	unopened	unknown cause	
5 May	67	–	–	–	–	–	–	–	–	8/12	8/12
8 May	31	–	–	–	–	–	1/3	–	–	–	1/3
12 May	20	4/20	–	–	–	–	–	–	–	–	4/20
13 May	12	–	–	–	–	–	–	–	–	1/8	1/8
15 May	20	–	–	–	–	–	–	–	–	4/20	4/20
19 May	20	–	–	–	–	–	–	1/5	–	–	1/5
29 May	20	4/20	–	–	–	–	–	–	–	1/5	5/25
5 June	20	5/25	–	–	–	–	1/5	–	–	–	6/30
12 June	20	6/30	–	–	–	–	–	–	–	–	6/30
19 June	20	19/95	1/5	–	–	–	–	–	–	–	20/100
26 June*	20	12/60	–	1/5	–	–	1/5	5/25	–	1/5	20/100
26 June**	20	15/75	–	–	–	1/5	1/5	–	–	–	17/85
3 July	20	13/40	–	–	–	–	–	–	–	3/15	17/85
17 July	20	7/35	–	1/5	–	1/5	1/5	6/30	–	1/5	17/85
Total (mean)+	80	11.7/58.8	–	0.5/2.5	–	0.5/2.5	1.0/5.0	2.7/13.7	–	1.2/6.2	17.7/88.8

*locality Brno-Jundrov
**locality Brno-Obřany
+from 26 June to 17 July inclusive

(90.0%) was localized in the basal third of the leaf blade (i.e. near a petiole) (Fig. 20).

In medium-aged and old poplars, galls of *P. gairi* (like galls of *P. spyrothecae*, *P. bursarius*, *P. populi* and *P. borealis*) occurred mainly in basal parts of the crown (up to a height of about 3.5 m). The characteristic ground localization of galls is obviously related to the most frequent places of egg wintering in fissures of rough bark.

Control factors

The population density of *P. gairi* is decreased by abiotic (mainly weather) and biotic (mainly the availability of suitable food and insect predators) factors. It is possible to suppose that (similarly as in other representatives of the family of Pemphigidae) considerable part (and sometimes also the majority) of eggs dies during the unfavourable winter period. However, also spring can be a critical period in the aphid development. During the long cold spring, larvae of fundatrices often hatch, however, due to the delayed unfolding of leaves they do not find suitable food and starve. Incoincidence of the period of leaf unfolding and the period of hatching the fundatrices can be one of the most important mortality factors. Cold and rainy weather in the period of aphid migration from primary hosts to secondary hosts and *vice versa* shows also unfavourable impacts on the abundance of *P. gairi*.

Fundatrices and fundatrigeniae live in galls which spontaneously open through fissure-shaped (or oval) emergence holes on the bottom side in the period of hatching the migrantes alatae. Galls protect very well their dwellers from drying out and unfavourable weather (above all rain), however, they are only little protected from insect and other natural enemies. Some enemies (e.g. Anthocoridae, Syrphidae, Chrysopidae and Aphidiidae) get into imperfectly closed galls through holes of various size (often hardly noticeable), other enemies (e.g. caterpillars of Lepidoptera) eat out the galls from without (or also from within) or peck out them (Aves). In galls on *P. nigra* in Brno, some 85 to 95% of aphids were killed through the cooperation of all mortality factors in

Table 14. The occurrence of *Anthocoris minki* in galls of *P. gairi* on leaves of *P. nigra* and *P. nigra* var. *italica*. Brno, 2003

Period		Number of galls	Galls with *Anthocoris* or exuviae		Galls with living nymphs		Galls with living imagoes	
			number	%	number	%	number	%
May	1st half	183	4	2.2	4	2.2	–	–
	2nd half	82	16	19.5	16	19.5	–	–
June	1st half	80	34	42.5	21	26.2	1	1.2
	2nd half	120	97	80.8	10	8.3	4	3.3
July	1st half	80	56	70.0	4	5.0	1	1.2
	2nd half	60	32	53.3	2	3.3	–	–
August	1st half	20	15	75.0	–	–	–	–
	2nd half	20	13	65.0	–	–	–	–
September	1st half	20	13	65.0	–	–	1	5.0
	2nd half	20	14	70.0	–	–	1	5.0
October	1st half	20	13	65.0	–	–	–	–
	2nd half	20	11	55.0	–	–	–	–
November	1st half	20	12	60.0	–	–	3	15.0

2003 (Table 12, Fig. 21). In galls on *P. nigra* var. *italica*, some 85 to 100% of aphids were killed by natural enemies (Table 13, Fig. 21). The greatest increase in the mortality of aphids in galls occurs in the 2nd half of May and in the 1st two decades of June, i.e. in the period of the intensive development of the 2nd generation of aphids.

Anthocoris minki

In Brno, the most important regulator of the abundance of *P. gairi* in galls was the predatory true bug *Anthocoris minki* Dohrn. (Anthocoridae Fig. – 22). Accidentally (i.e. out of the main terms of inspections), in galls on *P. nigra* var. *italica* in Brno-Obřany, *Heterorius laticollis* (Reut.) (Anthocoridae) was found. In the list of Heteroptera by HOBERLANDT in DLABOLA (1977), the species is not mentioned and, therefore, it is evidently its first find in the region of Moravia. *A. minki* is a common predator of

P. spyrothecae in galls on *P. nigra* and *P. nigra* var. *italica* (TÓTH 1939; DUŠEK, KŘÍSTEK 1959; URBAN 2002). It winters in the stage of imago and after wintering before reproduction, it feeds on free-living insects. It lays eggs either individually or in small open groups on galls or near galls on host plants. Hatched nymphs are very small and, therefore, they can penetrate into galls even through minute holes. They undergo their entire next development in galls.

The first specimens of *A. minki* (larvae of the 1st instar) were found in analyzed galls on *P. nigra* on 19 May and in galls on *P. nigra* var. *italica* as early as on 12 May. From this moment, the proportion of galls with heteropterans rapidly increased and as early as the 2nd half of June it reached 60 to 100% (on average 81.5%) (Tables 12 and 13). Nymphs were found in galls until 28 July, i.e. for the period of nearly 2.5 months. The greatest proportion of galls with living nymphs (26.2%) was noted in the first half of June. However, adults of *A. minki* were found in galls rarely and irregularly, viz. from mid-June till the beginning of November (Table 14). After sampling, adults left often the galls and only exuviae of the last nymphal instar gave evidence of their previous occurrence in galls.

A. minki of the 1st instar begins to occur sporadically in galls already in the period of the occurrence of the 4th in-
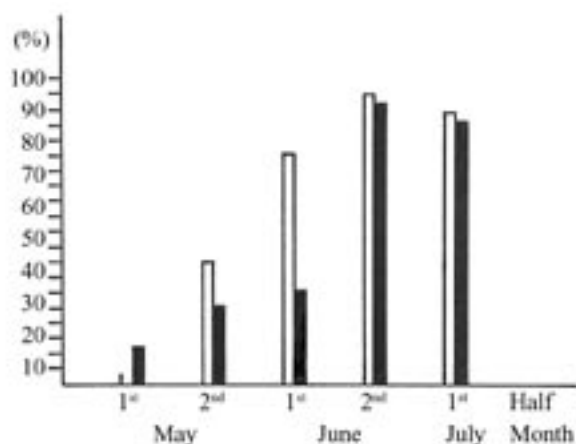

Fig. 21. Increase in the percentage of galls with the disturbed development of *P. gairi* on *P. nigra* in Žabovřesky (light) and on *P. nigra* var. *italica* in Obřany (dark). Brno, 2003
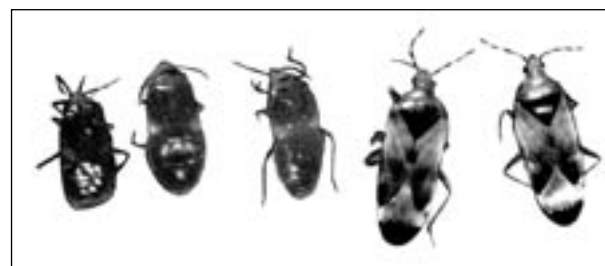

Fig. 22. Three nymphs of the 5th instar and two imagoes of *Anthocoris minki* Dohrn. (Anthocoridae)
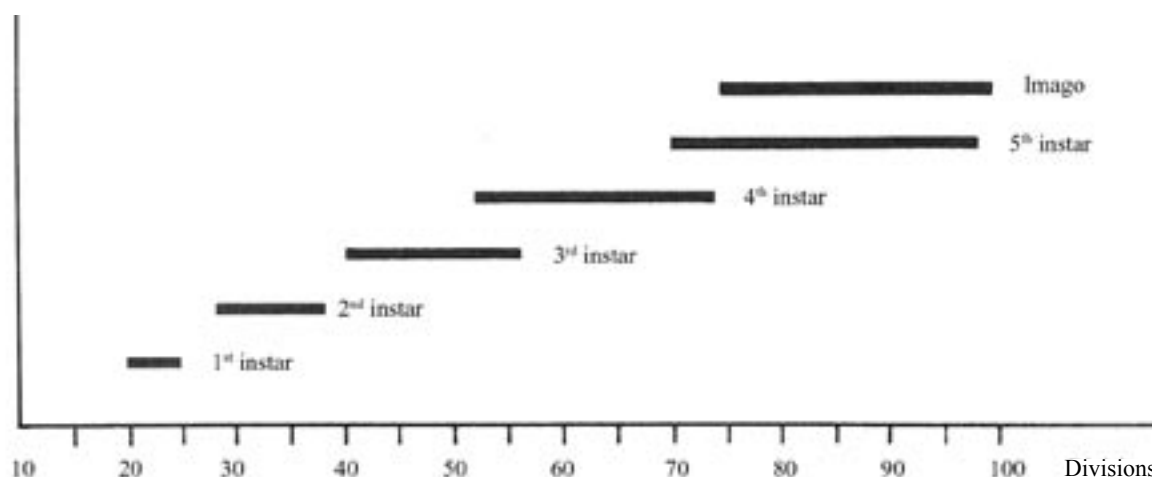
Fig. 23. Length of larvae, exuviae and imagoes of *A. minki* (1 division = 0.0357 mm). Brno, 2003
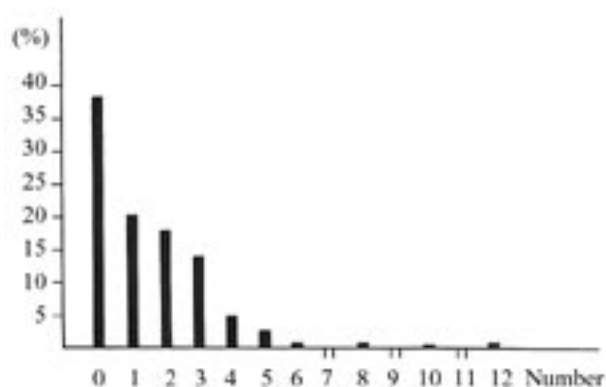

Fig. 24. Frequency of the occurrence of a various number of exuviae of *A. minki* in galls of *P. gairi* on leaves of *P. nigra* and *P. nigra* var. *italica*. Brno, 9 June to 8 September 2003 inclusive

star of fundatrices. These bugs always leave the galls after sucking up the fundatrices penetrating into other galls with living aphids. The majority of galls of *P. gairi* is, however, occupied by the heteropterans not until fundatrigeniae of the 1st to the 4th instar or even migrantes alatae occur. The bugs then usually first (in the course of several few days) kill all aphids of the 2nd generation and finally even the fundatrices. At the beginning of June or in July, it is possible to find even more than 100 dead fundatrigeniae including migrantes alatae and still living fundatrices in galls occupied by *A. minki*. However, the numerous colony of *P. gairi* in the initial period of its development in galls is not usually the sufficient source of food for the whole development of one true bug. Therefore, in the majority of galls (87.5%), only one nymph (or imago) of the heteropteran occurred and only in 10.4% of galls two heteropterans and in 2.1% of galls three heteropterans. In case of the numerous occupation of galls, heteropterans always leave the galls and complete their development in other galls with live colonies of aphids.

A. minki moults 5-times in galls during 5 to 7 weeks (Fig. 23). In the majority (61.7%) of analyzed galls, exuviae of heteropterans occurred, viz. in a number of 1 to 12 pieces (Fig. 24). In 33.3% of galls with sucked up aphids, 1 exuvia occurred, in 29.2% of galls 2 exuviae, in 22.4% of galls 3 exuviae, in 7.3% of galls 4 exuviae, in 4.6% of galls 5 exuviae and in 3.2% of galls 6 to 12 exuviae. Based on the frequency of the occurrence of exuviae of heteropterans in galls of *P. gairi* it is evident that the predominant part of nymphs and adults of *A. minki* migrates for food. Large colonies with full-grown fun-

Table 15. Relationship between a) length of galls and b) width of galls of *P. gairi* on leaves of *P. nigra* and *P. nigra* var. *italica* and the occurrence of exuviae of *Anthocoris minki*. Brno, from 9 June to 8 Sept. 2003 incl.

	Length (width) of galls (mm)	Total number of galls	Galls with exuviae		Mean number of exuviae	
a	≤ 10	65	37	56.9	1.0	1.8
	11–12	178	105	59.0	1.5	2.5
	≥ 13	112	77	68.8	1.7	2.5
	Total	355	219	61.7	1.5	2.4
b	≤ 4	147	84	57.1	1.3	2.3
	4.5–5	135	90	66.7	1.7	2.5
	≥ 5.5	73	45	61.6	1.4	2.3
	Total	355	219	61.7	1.5	2.4

Table 16. Number and dimensions (length/width) of galls with intact development of *P. gairi* and galls occupied by *Anthocoris minki* on leaves of a) *P. nigra* in Brno-Žabovřesky, b) *P. nigra* var. *italica* in Brno-Obřany in 2003

	Date	Number of galls		Length/width of galls (mm)	
		with intact development	with *Anthocoris*	with intact development	with *Anthocoris*
a	19 May	7	3	10.8/4.2	10.5/4.2
	26 May	8	9	11.9/4.7	11.7/4.8
	2 June	5	9	11.8/5.6	11.9/5.2
	9 June	2	16	12.0/6.0	11.9/4.7
	16 June	1	17	12.0/6.0	11.1/4.5
	23 June	1	18	10.0/4.0	11.7/4.8
	Total	24	72	11.5/4.9	11.6/4.7
b	29 May	14	4	12.6/4.9	11.6/4.0
	5 June	14	5	12.0/5.2	12.0/5.2
	12 June	14	6	12.0/5.5	10.8/5.0
	26 June	3	15	14.0/5.5	12.7/5.4
	Total	45	30	12.3/5.2	12.1/5.1

datrigeniae, however, can sustain as many as 2 (2.4) heteropterans.

It has been found that the average percentage of galls with exuviae of *A. minki* and the average number of exuviae in galls increase with the increasing length of galls (Table 15). It is evidently because with the increasing length of galls the length of fissure-shaped caps of galls on the abaxial face of leaves increases and thus, the probability increases of the origin of sufficiently large holes for penetrating *A. minki* into galls and for their leaving. A similar dependence has not been, however, proved between the width of galls and the percentage of galls with exuviae or the average number of exuviae of *A. minki* in galls. The results positively support an assumption that galls of the smallest width (height) category are least occupied by heteropterans (Table 15).

A. minki occupies galls mainly at the end of May in the first two decades of June (Tables 12 and 13), i.e. in the period of the coincident occurrence of all instars of fundatrigeniae including migrantes alatae. As a matter of fact, it refers to galls with completed growth (Table 9) and so killing the aphids does not affect the size or shape differentiation of galls. Average dimensions (length and width) of galls with the intact development of aphids and galls with sucked up aphids are thus the same (Table 16).

A. minki in galls of *P. gairi* kills always the whole colony of aphids. Larvae and adults leave galls after sucking up aphids. Sometimes holes serving for the penetration of heteropterans into galls close or do not increase during their stay in galls. Thus, heteropterans cannot leave galls after the consumption of food. For a certain time, starving nymphs (or freshly hatched adults) of heteropterans live thanks to the consumption of excrements of aphids, however, finally they die. Mortality of "imprisoned" *A. minki* caused by starvation in galls (sporadically also

by other reasons) is, however, very low (5.2%) affecting mainly (80%) nymphs.

Lepidoptera

Galls of *P. gairi* on leaves of *P. nigra* (rarely also *P. nigra* var. *italica*) are damaged by caterpillars of several species of moths (Lepidoptera). In galls on *P. nigra* in Brno-Žabovřesky, small phyllophagous caterpillars developed of *Batrachedra praeangusta* (Haw.) (Batrachedridae) and *Gypsonoma minutana* (Hbn.) (Tortricidae). From galls on *P. nigra* var. *italica* in Brno-Jundrov, moths were reared of *Adoxophyes orana* (Fisch. v. R.) (= *reticulana* /Hbn./) (Tortricidae).

Caterpillars eat out surface sockets of a diameter of 0.4 to 1 (on average 0.8) mm in galls and holes of

Fig. 25. A gall of *P. gairi* on the leaf of *P. nigra* var. *italica* damaged by caterpillars of a moth (Lepidoptera) and of *Idiocerus* sp. (Cicadellidae). Brno-Obřany, 5 June 2003

Table 17. Galls of *P. gairi* on leaves of *P. nigra* damaged by caterpillars of Lepidoptera. Brno-Žabovřesky, 2003

Date	Total number of galls	Galls eaten up from within		Galls with sockets and holes		Total number	
		number	%	number	%	sockets	holes
26 May	20	1	5	1	5	2	1
2 June	20	3	15	5	25	10	6
9 June	20	3	15	6	30	33	14
16 June	20	1	5	2	10	12	2
23 June	20	–	–	2	10	8	2
30 June	20	3	15	6	30	23	8
7 July	20	7	35	7	35	30	10
10 July	20	4	20	9	45	45	7
14 July	20	3	15	12	60	40	20
21 July	20	7	35	11	55	35	11
28 July	20	5	25	14	70	36	22
11 August	20	7	35	20	100	123	23
25 August	20	10	50	11	55	30	13
8 Sept.	20	10	50	13	65	41	15
22 Sept.	20	8	40	18	90	63	12
6 Oct.	20	6	30	12	60	46	11
20 Oct.	20	12	60	15	75	35	10
3 Nov.	20	10	50	14	70	85	9
Mean*	–	5.2	26.2	10.6	53.0	1.9	0.7
Mean**	–	9.0	45.0	14.7	73.6	3.0	0.7

* from 7 July to 21 July incl.
** from 11 August to 3 November inclusive

a diameter of 0.5 to 3 (on average 1.2) mm (Figs. 25 and 26). Through the holes (or through holes eat out from the

Fig. 26. A gall of *P. gairi* on a leaf of *P. nigra* var. *italica* with a hole eaten up by the moth caterpillar (Lepidoptera). Brno-Obřany, 5 June 2003

adaxial face of leaves to a fissure-shaped cap) they often penetrate into galls. In galls, they kill all aphids and eat out inner walls of galls in irregular plots. Partly grown or almost grown-up caterpillars usually leave the galls and complete their feeding on leaves. Grown-up caterpillars spin a whitish cocoon, viz. usually on the abaxial face of leaves near the fissure-shaped mouth of galls (Fig. 27). Feeding marks usually affect 1/4 to 2/3 of the inner area of galls. The thickness of gall walls is substantially reduced (even by 50%) at the place of feeding. Light-yellow-green inner walls of galls soon become darker after damage. Galls abandoned by caterpillars can be easily identified also according to characteristic dark frass and thin whitish web.

Damage to galls of *P. gairi* by caterpillars of Lepidoptera began on 26 May. The proportion of galls eat out from within by caterpillars increased in next months till autumn. According to inspections carried out from 7 to 21 July, about 26.2% of galls were eat out by the caterpillars. Considerable part (28.6%) of eat out galls was already previously occupied by *A. minki*. It means that caterpillars killed aphids actually "only" in 15% of galls. In checks carried out from 11 August to 3 November inclusive, caterpillars ate out (from within) about 45.0% of all galls (Tables 12 and 17). Within the period, caterpillars damaged in total (from without and from within) on average 73.6% of all galls. On average 3 sockets and 0.7 holes

Table 18. Damage to leaf blades of *P. nigra* by caterpillars of *Batrachedra praeangusta* and *Gypsonoma minutana*. In addition to leaf blades, caterpillars damaged about 73.6% of galls of *P. gairi* of which about 45% were eaten up from within. Brno-Žabovřesky, 2003

Damage to leaf blades	21 July	25 Aug.	8 Sept.	Total	%
Skeletonization from an adaxial face	13	9	12	34	41.4
Skeletonization from an abaxial face	8	4	6	18	22.0
Skeletonization both from the adaxial and abaxial faces	7	4	3	14	17.1
Perforation	4	3	2	9	11.0
Skeletonization and perforation	2	1	2	5	6.1
Undamaged	1	–	1	2	2.4
Total	35	21	26	82	100.0

occurred in analyzed galls (Table 17). Based on data in the table it is evident that in the period 7–21 July inclusive, only incomplete half (49.1%) of galls damaged by sockets and holes was eaten out by caterpillars from within. The percentage of galls with various numbers of sockets and holes eaten out by caterpillars of *B. praeangusta* and *G. minutana* is shown in Fig. 28.

In *P. nigra* in Brno-Žabovřesky, in addition to galls also leaf blades were damaged (in 97.6%) by caterpillars of *B. praeangusta* and *G. minutana* (Table 18). In total, 41.4% leaves were damaged by skeletonization from the adaxial face, 22.0% from the abaxial face and 17.1% from both faces. Less frequently (in 11.0%), leaves were damaged by perforation and rather rarely (in 6.1%) by skeletonization and perforation. Damage to particular leaves never exceeded 4% of their area and the average damaged area (about 0.2%) was negligible. Even under so low scattered feeding, caterpillars damaged leaf blades of nearly all (97.6%) leaves with galls of *P. gairi* and also the majority (about 73.6%) of galls. Marks of feeding were noticed also on nearly all leaves without galls. Nevertheless, it is possible to note that galls of *P. gairi* are a rather attractive source of food and a suitable place of shelter for caterpillars of moths mentioned above.

Galls eaten out by moths caterpillars from within die (and subsequently become brown or even turn black) usually sooner than undamaged galls. The percentage of dying and dead galls of *P. gairi* not eaten out and eaten out by caterpillars is depicted in Fig. 29.

Other insect natural enemies

The proportion of other insect enemies in the mortality of *P. gairi* in galls on *P. nigra* and *P. nigra* var. *italica* in Brno was only negligible (Tables 12 and 13). About 2.5 to 3.3% of aphids were killed by larvae of the family Chrysopidae (Neuroptera) either separately or in combination with *A. minki*. In 0 to 5% of galls on *P. nigra*, an unspecified endoparasitoid from the family Aphidiidae developing in fundatrices occurred together with *A. minki*.

Heringia heringi (Zett.) and *Pipiza festiva* Meig. (Syrphidae) ranked among infrequent predators occurring in less than 5% of galls. Both species are common predators of aphids from the genus *Pemphigus* (DUŠEK, KŘÍSTEK

1959). They are adapted to develop in their cecidia and so they cannot develop on freely living colonies of aphids (DUŠEK, LÁSKA 1966). In Brno, the predators were found in even 30.4% of galls on *P. nigra* and in as many as 6.8% of galls on *P. nigra* var. *italica* (URBAN 2002). Both species show similar bionomy. They winter as grown-up larvae, viz. usually out of galls. Adults feed on pollen or flower nectar in spring and in the course of maturation feeding they sexually mature. They lay chalky eggs most frequently into a gall fissure on the abaxial face of leaves. Larvae penetrate into galls through small primary fissures. In the galls, they gradually suck aphids and grow up in the 3rd instar. According to KURIR (1963), they further develop after a 7 to 8-month winter diapause showing univoltine development. However, the statement contradicts with a fact that part of the larvae of *H. heringi* hatched in our laboratory rearing without a diapause as early as September.

Aves

In studied localities, birds (and of these mainly titmouse *Parus major*) pecked out 1.7% of galls of *P. gairi* on *P. nigra* and 13.7% of galls on *P. nigra* var. *italica* (Tables 12 and 13). Pecking out the galls began on 19 May and finished in mid-July. Galls were most frequently pecked out in the 2nd half of June when the weight of the living aphid biomass (or that of killed *A. minki*) culminated. The pecked out holes were on average 3.4 mm long and 2.6 mm wide. No significant differences were found in the size of pecked out and non-pecked out galls.

Defects in gall opening

At the end of May and at the beginning of June, the majority of galls opens on the abaxial face of leaves (i.e. in the place of a fissure-shaped cap). Through fissure-shaped or oval holes, aphids begin to remove abundantly produced "honeydew" and numerous exuviae. The holes also serve to aphids for the control of air humidity and mainly for the emergence of migrantes alatae. Aphids suck and produce excrements also in case of late or insufficient opening the galls. Growing aphids and their excrements with exuviae fill up the inner space of closed galls. The living space of aphids in the galls rapidly diminishes and

Fig. 27. Abaxial face of the leaf of *P. nigra* with a whitish co-coon, frass in thin web and caterpillar feeding of *Batrachedra praeangusta* (Haw.) (Batrachedridae) on the leaf of *P. nigra*. A gall of *P. gairi* eaten up by a caterpillar occurs on the adaxial face of a leaf. Brno-Žabovřesky, 12 June 2003

the environment deteriorates. Debilitated aphids finally die due to "drowning" in their own excrements or under synergism of the causal agents of diseases (bacteria, ento-mophagous fungi and polyhedral viruses). While viruses attack debilitated and so far living aphids, bacteria and fungi colonize also dead aphids.

In consequence of disorders in opening the galls aphids died in 1.7% of analyzed galls on *P. nigra* and in 0% galls on *P. nigra* var. *italica* (Tables 12 and 13). According to RUPAJS (1989), gall generations of a related *P. populini-*

grae (Schr.) often die in their own excrements. Defects in opening the galls belong to rather important control factors of *P. spyrothecae*. For example in Brno, they killed aphids in 7.8% of galls on *P. nigra* and in 19.5% of galls on *P. nigra* var. *italica* (URBAN 2002).

Unknown causes

In 0.8% of galls of *P. gairi* on *P. nigra* and in 6.2% of galls on *P. nigra* var. *italica*, it was not possible to find reliably causes of the aphid death. Mostly it referred to the death of the 1st and 2nd instars of fundatrices which was probably caused by insect predators (mainly by *A. minki*).

Factors not affecting the development of *P. gairi*

From 8 May to 2 June, shiny colourless eggs (later on chorions of hatched eggs) of *Idio-cerus* sp. (Cicadel-lidae) were found on walls of studied galls of *P. gairi*. In total, *Idiocerus* laid eggs on about 1.5% of galls in *P. nigra* and 1.5% of galls in *P. nigra* var. *italica*. Some 1 to 10 (on average 4) eggs were laid into galls. The eggs reached a length of about 1.15 mm and width of about 0.3 mm. They were usually embedded into galls at their top where walls are thickest. Ends of the eggs often slightly protruded either outwards or inwards of the galls. Notches on the surface of galls were 1 to 2.9 (on average 1.5) mm long. The surface of egg-laid galls was wrinkled and covered with brownish callus (Fig. 25). The laying and development of *Idiocerus* sp. eggs obviously did not affected the development of *P. gairi*.

From 3 July, spiders (Araneida) began to occur in analyzed galls of *P. gairi*. Until the end of August, the proportion of galls occupied by spiders increased to 5%. In September and October, the percent of galls with spiders rapidly increased and at the end of October or at the beginning of November, spiders (or their exuviae) occupied about 20% of all galls. In one gall, always maximally one spider (or exuvia) was present. Spiders usually occurred in already abandoned galls their control importance being quite negligible.
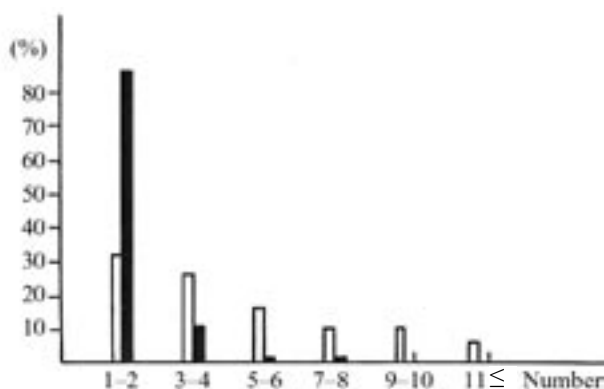

Fig. 28. The percentage of galls of *P. gairi* with the various number of sockets (light) and holes (dark) eaten up by caterpillars of Lepidoptera on leaves of *P. nigra*. Brno-Žabovřesky, 28 July to 20 October 2003 inclusive
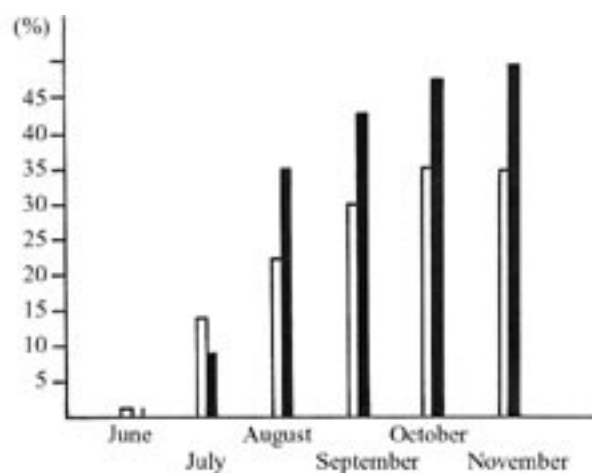

Fig. 29. The percentage of dying and dead galls of *P. gairi* on leaves of *P. nigra* not eaten up (light) and eaten up by caterpillars of Lepidoptera (dark). Brno-Žabovřesky, 2003

Harmfulness

P. gairi (similarly as the majority of other cecidog-
enous species of aphids) migrates from primary hosts to
secondary hosts. On primary hosts (*P. nigra* and *P. nigra*
var. *italica*) it develops in leaf galls, on secondary hosts
(*Aethusa cynapium*) it lives freely on roots. A certain
(although only small or even negligible) economic im-
portance can be only on primary hosts. Under heavy
attack, it physiologically weakens trees and, moreover,
in *P. nigra* var. *italica* decreases their decorative value
or due to "honeydew" it pollutes the environment. The
harmfulness of *P. gairi* on *P. nigra* is nearly negligible.
In the poplar, galls die usually much later than in *P. nigra*
var. *italica* and, therefore, they often assimilate until the
autumn leaf-fall.

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Výskyt, vývoj a přirození nepřátelé cecidogenních generací *Pemphigus gairi* Stroyan (Sternorrhyncha, Pemphigidae)

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ABSTRAKT: Práce pojednává o výskytu, vývoji a přirozených nepřátelích hálkotvorné *Pemphigus gairi* Stroyan (Pemphigidae). Tato dutilka se v roce 2003 hojně vyskytovala na listech *Populus nigra* a *P. nigra* var. *italica* v Brně. Byla popsána z Anglie a o jejím výskytu z kontinentální Evropy nejsou v dostupné literatuře žádné zprávy. Jedná se o holocyklický a heteroekní druh. Na sledovaných lokalitách se larvy fundatrices líhly hlavně v poslední dekádě dubna. Jejich sáním na abaxiální straně čerstvě vyrašených listů topolů vznikají na adaxiální straně listů (poblíž střední listové žilky) druhově nespecifické podélné taškovité hálky. Během 12 až 14 dnů fundatrices dospívají v hálkách o průměrné délce 11,2 mm a šířce 3,9 mm. Imaga žijí kolem 1,5 měsíce, a to nejdéle do poloviny července. Zplodí v průměru 75,6 fundatrigenií, které během 16 dnů dospívají v okřídlené migrantes alatae. V době líhnutí prvních migrantů (koncem května) hálky dorůstají konečné délky kolem 11,8 mm a šířky 4,7 mm. V primárních štěrbinovitých uzávěrech se na abaxiální straně listů otevírají a vzniklými výletovými otvory migranti hálky opouštějí. Na sekundárním hostiteli (*Aethusa cynapium,* Daucaceae) zplodí průměrně kolem 17,5 larev exules. Vlivem přirozených nepřátel (především ploštice *Anthocoris minki*) hynou mšice v 90 % hálek.

Klíčová slova: *Pemphigus gairi*; *Populus* spp.; výskyt; vývoj; hálky; nepřátelé; *Anthocoris minki*; význam

Pemphigus gairi Stroyan je holocyklický a heteroekní zástupce čeledi dutilkovití Pemphigidae. Má jednoletý vývoj, během něhož migruje z listových hálek na primárních hostitelích (*Populus nigra* L. a *P. nigra* L. var. *italica*) na kořeny sekundárního hostitele (*Aethusa cynapium* L.). Druh byl popsán v Anglii a o jeho výskytu v kontinentální Evropě zřejmě dosud neexistují písemné zprávy. V ČR jej však na uvedených hostitelích nalezl poblíž Prahy Dr. J. Holman (písemné sdělení, 2003).

V roce 2003 se hálky *P. gairi* hojně vyskytovaly na středně starých a starších topolech *P. nigra* a *P. nigra* var. *italica* v Brně. Z obou těchto taxonů byly během vegetační sezony odebírány hálky k laboratornímu vyšetření. Kromě metrických znaků (plochy postižených listů, délky, šířky a výšky hálek a tloušťky jejich stěn) byl zjišťován také vývojový stupeň a velikost (délka, šířka těla, příp. šířka crania) fundatrice a fundatrigenií včetně migrantes alatae. Pitvou ovarií přirozeně uhynulých fundatrices a dospělých migrantes alatae byl vyšetřován počet nezplozených larev. Z počtu zplozených a nezplozených larev byla odvozována natalita samiček. Průběžná pozornost byla věnována mortalitním faktorům mšice. Byly získány tyto hlavní poznatky:

1. Fundatrices se na zkoumaných lokalitách líhnou ve druhé polovině dubna. Usazují se na abaxiální straně rašících a čerstvě vyrašených listů poblíž střední listové žilky. Jejich sáním se na protější (tj. adaxiální) straně listů vytvářejí podélně ovalné měchýřkovité vychlípeniny. Ty se ve spodní části brzy štěrbinovitě uzavírají, takže již fundatrices 2. instaru sají v prostorné vnitřní dutině hálek. Hálky vytváří jedna fundatrix, pouze v počátečním období sání (až do 3. instaru) se na tvorbě

6,3 % hálek podílejí 2 až 3 fundatrices. Vlivem kompetice se dále vyvíjí pouze jedna fundatrix.

2. Fundatrices se rychle vyvíjejí a po čtyřech svlékáních dospívají. První imaga se v analyzovaných hálkách objevila již 9. května, tj. po 12 až 14 dnech od počátku sání 1. instaru. Zhruba za dva dny od vylíhnutí se imaga začnou rozmnožovat. Samičky žijí v průměru 1,5 (maximálně 2) měsíce, a to nejdéle do poloviny července. Jejich fyziologická plodnost je 32 až 157 (průměrně 75,6) larev (fundatrigenií). Po skončení rozmnožování zůstává v ovariích kolem 5,8 % nenarozených larev (ekologická plodnost se blíží plodnosti fyziologické).

3. Fundatrigenie se na zkoumaných lokalitách vyskytovaly od 11. května do 31. července. Během asi 16denního vývoje se čtyřikrát svlékaly a první migrantes alatae se vyskytly 27. května. Od konce května až do poloviny července se v hálkách spolu s fundatrices vyskytovaly všechny instary fundatrigenií včetně migrantes alatae.

4. Fundatrigenie vylučují množství kapénkovitých exkrementů, které se často slévají dohromady a (spolu s četnými exuviemi) se hromadí v hálkách. Koncem období vývoje tohoto pokolení je v hálkách 1 až 800 (průměrně 600) kulovitých kapének o průměru 0,11 až 2,14 mm. S pokračujícím vývojem se životní prostor fundatrigenií zmenšuje a životní podmínky se zhoršují. V době líhnutí prvních migrantes alatae (v Brně od 25. května) se hálky začínají v primárních štěrbinovitých uzávěrech postupně otevírat. Začátkem června je většina hálek otevřena úzkou štěrbinou, příp. podélně ovalnými výletovými otvory. Uzavřeno zůstává kolem 4,6 % hálek. Kromě výletu migrantů otvory slouží také k odvětrávání vnitřního prostoru

hálek a k odstraňování exkrementů, exuvií a uhynulých fundatrices z hálek.

5. Migrantes alatae nepřijímají potravu a po několika dnech dospívají. Jejich ovaria obsahují 10 až 30 (průměrně 17,5) vzrostlých larev 1. instaru. Největší samičky mají (proti nejmenším samičkám) až trojnásobnou natalitu. V červnu a červenci přelétávají na kořeny sekundární hostitelské rostliny (*Aethusa cynapium*, Daucaceae), kde se vyvíjí pokolení exules. Okřídlení virginogenní jedinci (tj. sexuparae, remigrantes alatae) pak v říjnu přelétají na topoly. Na jejich kůře plodí larvy, které dospívají v apterní samečky a samičky pokolení sexuales. Oplodněné oviparní samičky sexuales vykladou do štěrbin kůry vždy jen jedno silnostěnné zimní vajíčko.

6. Hálky *P. gairi* jsou prakticky nerozlišitelné od hálek *P. populinigrae* (Schr.), *P. phenax* Börn. et Blunck) a *P. passeki* Börn. Těsně před počátkem rozmnožování fundatrices dosahují průměrné délky 11,2 mm a šířky (i výšky) 3,9 mm. V době líhnutí prvních migrantů dorůstají konečné délky kolem 11,8 mm a šířky 4,7 mm. Od 1. dekády května do konce června vzroste průměrná tloušťka hálkové stěny při vrcholu z 0,64 (při bázi z 0,38) mm na 1,25 (při bázi na 0,61) mm. Přitom průměrná tloušťka nepoškozených listových čepelí je kolem 0,12 mm a během vegetační doby se téměř nemění. S velikostí čepele průkazně vzrůstá velikost hálek.

7. Hálky jsou žlutozelené, hladké, někdy částečně načervenalé. Po opuštění mšicemi od poloviny června postupně odumírají. Odumírání (a související hnědnutí až černání) hálek postupuje na *P. nigra* (oproti *P. nigra* var. *italica*) mnohem pomaleji, takže velká část hálek odumírá až po podzimním opadu listů. Na jednom listu bývá zpravidla (v 96,5 %) jen jedna hálka. Na *P. nigra* bylo 72,2 % hálek lokalizováno ve střední třetině listové čepele. Na *P. nigra* var. *italica* bylo 90,0 % hálek lokalizováno v bazální třetině čepele, přičemž průměrná plocha čepele byla (oproti *P. nigra*) zhruba poloviční.

8. V hálkách *P. gairi* na *P. nigra* bylo mortalitními faktory zahubeno 85 až 95 % mšic a v hálkách na *P. nigra* var. *italica* 85 až 100 % mšic. Nejúčinnějším regulátorem byla dravá ploštice *Anthocoris minki* Dohrn. (Anthocoridae), která zahubila mšice průměrně v 81,5 % vyšetřovaných hálek. Její larvy byly v hálkách nalézány od 12. května do 28. července, imaga od poloviny června do začátku listopadu. V 87,5 % obsazených hálek byla jedna ploštice, v 10,4 % hálek dvě ploštice a ve 2,1 % hálek tři ploštice. Během pěti- až sedmitýdenního vývoje se ploštice pětkrát svléká. Exuvie byly nalezeny v 61,7 % všech vyšetřovaných hálek. Ve 33,3 % hálek s vysátými mšicemi byla jedna exuvie, ve 29,2 % hálek dvě exuvie, v 22,4 % hálek tři exuvie, v 7,3 % hálek čtyři exuvie, ve 4,6 % hálek pět exuvií a ve 3,2 % hálek šest až 12 exuvií. Z frekvence výskytu exuvií vyplývá, že ploštice za potravou migruje. Avšak početné kolonie mšic se vzrostlými fundatrigeniemi mohou uživit až dvě ploštice. Ploštice hubí mšice v již dorostlých hálkách, a proto se úhyn mšic neprojevuje ve velikostní diferenciaci hálek.

9. Hálky na *P. nigra* byly zevně i zevnitř hojně poškozovány housenkami motýlů *Batrachedra praeangusta* (Haw.) (Batrachedridae) a *Gypsonoma minutana* (Hbn.) (Tortricidae). Hálky na *P. nigra* var. *italica* byly poškozovány jen zřídka, a to housenkami *Adoxophyes orana* (Fisch. v.R.) (Tortricidae). Při vyžírání vnitřních stěn hálek byly mšice vždy zahubeny. Na *P. nigra* bylo jimi do 21. července vyžráno kolem 26,2 % hálek a do 3. listopadu kolem 45,0 % hálek. Část vyžraných hálek však byla již předtím obsazena *A. minki*, a proto ve skutečnosti housenky zahubily mšice „jen" v asi 15 % hálek.

10. K řídkým predátorům *P. gairi* náležely *Heringia heringi* (Zett.) a *Pipiza festiva* Meig. (Syrphidae), které zahubily mšice v téměř 5 % hálek. Na mortalitě mšic se dále asi 3 % podílely larvy blíže neurčeného druhu z čeledi Chrysopidae. Zhruba stejně hojný úhyn působil endoparazitoid fundatrices z čeledi Aphidiidae. Ptáci (Aves) (hlavně sýkory) vyklovali kolem 1,7 % hálek na *P. nigra* a kolem 13,7 % hálek na *P. nigra* var. *italica*. V důsledku poruch v otevírání hálek se ve vlastních exkrementech „utopily" mšice v 1,7 % hálek na *P. nigra*. Ve stěnách 1,5 % vyšetřovaných hálek na obou topolech byla nalézána vajíčka kříska *Idiocerus* sp.

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