

DIPLOLEPIS ROSAE (L.) (HYMENOPTERA: CYNIPIDAE): DEVELOPMENT, ECOLOGY AND GALLS IN THE BRNO REGION

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Abstract

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The paper results from two years of studying development and formation of the galls of *Diplolepis rosae* (L.) on *Rosa canina* (L.) in the Brno region (Czech Republic). Following the extremely warm and dry growing season of 2015, 70% of prepupae and 30% of grown-up 2nd instar larvae hibernated. After the climatically milder growing period of 2016, only 47% of prepupae and 53% of grown-up larvae hibernated. Pupae were recorded from mid-March to mid-July and imagoes occurred from April to July. The average percentage of males in the populations was 4.5%. Eggs were found in the galls from May to July. Larvae of the 1st and 2nd instars were found in the galls from June to August and from July to October (or to next March), respectively. Average cranium width in the 1st instar larvae increased during the growth of larvae from 0.25 to 0.35 mm, i.e. by 38%. Average cranium width in the 2nd instar larvae was 0.55 mm and practically did not change during the growth of the larvae. 85.1% of galls were formed on budding leaves, 14.9% on flowers and fruits. The galls were growing most rapidly in June and July, and their growth ended in October when they reached average height and width of 40 mm and 47 mm, respectively. They consisted of 1 to 20 (on average 7) \pm intergrown parts with 1 to 225 (on average 54) cells. 63.5% of them were localized along the sides of shoots and 36.5% were found on the shoot tips. The largest cells (3.9 x 3.1 mm) were those with the completed development of gall wasp larvae. Cells inhabited by parasitoids were by 15.0% smaller and by 24.5% smaller were cells with dead gallwasp larvae due to natural reasons. As compared with the cells with the completed development of gall wasp, cells with the larvae of inquiline *Periclistus brandtii* (Ratz.) were by 43.6% shorter and by 50.6% narrower. The inquiline was found in 10% of galls and in 3.6% of cells. In 2015, parasitoids inhabited on average 15.0% (in 2016 22.1%) of cells. Approximately 50% of the population of *D. rosae* died in the galls during the preimaginal development.

Keywords: *Diplolepis rosae*, *Cynipidae*, hibernation, development, galls, inquiline *Periclistus brandtii*, mortality

INTRODUCTION

Gall wasp *Diplolepis rosae* (Linnaeus, 1758) (syn. *Cynips rosae*, *Rhodites rosae*, *Diplolepis bedeguaris*) is the most common representative of the genus *Diplolepis* Geoffroy, 1762. This cecidogenous

genus, classified within the Diplolepini tribe, is represented in the Palearctic region by approximately 16 species living exclusively on roses (*Rosa* spp.), on which they form species-specific galls. From ten European species (Kovalev, 1981) and

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six native species (Mikula, 1989), galls of *D. rosae* are most conspicuous and usually also most abundant. Biogeography, hosts, abundance, formation of galls and natural enemies of gall wasp are subjects of numerous studies some of which are older than 120 years. Recently in particular, many authors study the abundant inquiline species of *Periclistus brandtii* (Ratz.) (Cynipidae: Synergini) and an endosymbiotic bacteria from the family of *Wolbachia* Hert. (Rickettsiales).

Despite the above-mentioned facts, there are still unresolved questions remaining in the biology of *D. rosae*, which particularly relate to the causes of gall formation, course of the development of individual evolution stages (and instars), genetic structure of populations and specific relation to various hosts. The submitted paper deals with the development of *D. rosae*, the size of its galls, number and size of cells. The main objective of the study was to determine the course of the development of larvae and the number of their instars.

Geographical distribution and host plants

Diplolepis rosae is a Holarctic species widely spread in the northern temperate zone. In the Palaearctic region, it occurs from North Africa, across West, Central and South Europe, reaching up to the European part of the former USSR. It is reported from Asia Minor, Western Asia, Central Asia and Eastern-Palaearctic subregion. In 1868, it was introduced into North America along with its main European host plant, i.e. *Rosa canina* L. (Weld, 1926; Judd, 1959). Hosts are numerous wild *Rosa* spp., on the leaves, flowers and fruits of which the gall wasp creates specific and very conspicuous galls. According to the *Rosa* family, the species was given valid generic scientific designation and name nearly in all national languages. The occurrence of *D. rosae* in Europe and North America on ten *Rosa* spp. was mentioned already by Dalla Torre (1893). Kovalev (1981) reported *D. rosae* from Europe and Kazakhstan on *Rosa canina* L., *R. arvensis* Huds., *R. pendulina* L., *R. micrantha* Sm. and *R. dumalis* Bechst. According to Darboux and Houard (1901), the species occurs in Europe and in the Mediterranean subregion on twenty *Rosa* spp. As host plants, the authors consider among others *R. canina* L., *R. agrestis* Savi, *R. arvensis* Huds., *R. dumalis* Bechst., *R. gallica* L., *R. glauca* Pourr., *R. inodora* Fries., *R. micrantha* Sm., *R. pimpinellifolia* L. and *R. rubiginosa* L., which are known from the Czech Republic, too.

The centre of the occurrence of *D. rosae* is in Europe (Kieffer, 1914; Escherich, 1942; Gauss, 1982). In northern Europe, its occurrence is limited to southern Scandinavia (Vyržikovskaja, 1962; Stille, 1984). In southern Sweden, galls were found apart from on *R. canina* also on *R. dumalis* Bechst., *R. rubiginosa* L., *R. villosa* L., *R. sherardii* Dav. and *R. glauca* Pourr., but not on *R. majalis* Herrm. and *R. rugosa* Thunb. (Stille, 1984). In Great Britain and Ireland, galls were most frequently found on the wild *R.*

canina (Redfern, 1997; Williams and Randolph, 2002; Ellis, 2004; O'Connor, 2004) and on *R. glauca* Pourr. (Bowdrey, 2007). The common occurrence of *D. rosae* on *Rosa* spp. in the open and its occasional occurrence on cultivated species are mentioned for example by Schröder (1967). Schröder (1967), Syrett (1990) and Herting (s. a.) consider *D. rosae* a species efficient in the biological control of *Rosa rubiginosa* L., widespread in New Zealand following the successful control of wild rabbit.

A number of studies on the occurrence and distribution of *D. rosae* originates from non-European countries. For example, Bayram, Ülgentürk and Toros (1998), Güçlü *et al.* (2008), and Katılmış and Kiyak (2010) studied the species in Turkey. The most abundant species in that country is however *D. fructorum* (Rübs.), which is taken for the pest on *Rosa* spp. fruits in plantations. Together with *D. mayri* (Schl.), it was introduced into Iran (Farahbakhsh, 1961), where it was later studied (Shojai, 1998; Hesami *et al.*, 2008). Gibson (1935) ranked it with the harmful species on *Rosa* spp. in Canada. According to Shorthouse (2001), it was introduced into Canada with its European host plants *R. canina* and *R. rubiginosa* and occurs there both on wild growing shrubs and on shrubs cultivated in gardens. The occurrence of *D. rosae* on *R. canina* L. and *R. rubiginosa* L. in the non-arctic region is reported e.g. by Judd (1959) and on *R. rubiginosa* L. by Ritchie and Peters (1981). Liu, Zhang and Xiao (2012) maintain that from North America it was introduced into China where it causes massive damage on *R. sertata* Rolfe × *R. rugosa* Thunb. for example in the province of Gans.

Entomologists dealing with faunistic studies of cecidogenous insect species in the Czech Republic were E. Bayer in 1909–1922 and E. Baudyš in 1913–1966. Thanks to their numerous findings on many *Rosa* spp., the occurrence of *D. rosae* is relatively well mapped. Recently, faunistics of gall wasps in the Podyjí National Park was studied by Holý (2011), who found *D. rosae* on a majority of 25 surveyed localities.

The current state of knowledge

Fundamental data on *D. rosae* can be found in many entomological and nature conservation compendia (Kieffer, 1914; Escherich, 1942; Miller, 1956; Gauss, 1982; Sedlag *et al.*, 1986 and others). Several researchers studied primarily its morphology and taxonomy (Dalla Torre and Kieffer, 1910; Ritchie and Peters, 1981; Nieves Aldrey, Vårdal and Ronquist, 2005), others focused on the formation of galls (Magnus, 1914; Shaeffer and Meyer, 1963; Redfern, 1997). Adler (1877), Callan (1940), Stille and Dävring (1980) dealt with reproduction and sexual behaviour, Bronner (1985) studied oviposition. Blair (1943, 1945, 1951), Randolph (2005) and others focused on *D. rosae* galls and biology. Vårdal, Sahlén and Ronquist (2003) studied the clutch size, size, shape and structure of eggs as well as the role of

embryos in the process of gall formation. László and Tóthmérész (2008) examined the optimal clutch size, which differs from the most frequently recorded number of laid eggs (25–30). According to them, the most frequently recorded clutch size is suboptimal in relation to the proportion of successfully hatched progeny. Stille (1984) found out that total parasitisation and mortality of *D. rosae* decrease with the increasing gall size. László and Tóthmérész (2007, 2011) studied parasitisation of galls and its relation to the size of galls and spatial distribution of shrubs of *Rosa* spp. The authors demonstrated among other that the density of galls and their parasitisation decrease with the increasing density of shrubs. Ferrari, Kruess and Tschamtker (1997) determined the influence of environment division and size of galls on their insect community.

Parasitoids of *D. rosae* and the inquiline species of *Periclistus brandtii* (Ratz.) (Cynipidae) were studied by Voukassovitch (1928), Judd (1959), Grigorov (1962), Nordlander (1973), Tudor and Caruntu (1980), Nieves Aldrey (1981), Doğanlar (1984), Bayram, Ülgentürk and Toros (1998), László (2001), Williams and Randolph (2002), László and Tóthmérész (2006, 2012, 2013a, b), Rizzo and Massa (2006), Hesami *et al.* (2008), Todorov *et al.* (2012), Liu, Zhang and Xiao (2012), Boyadzhiev and Todorov (2013), László, Rákossy and Tóthmérész (2014), Chireceanu *et al.* (2015), Mete and Mergen (2016) and others. Communities of various Hymenoptera species associated with the galls of little known *D. mayri* (Schl.) are mentioned by Askew, Sadeghi and Tavakoli (2006). Hintze-Podufal and Thiele (1998) compared the microfauna of grown-up and old galls after their hibernation. Blommers (2008) studied the occurrence of so-called successor insect species in the cavities of galls deserted by gall wasps *D. rosae* and their parasitoids and inquilines. Valuable are findings on the occurrence, hosts and biology of less known related species of *D. japonica* (Walk.) (Yasumatsu and Taketani, 1967). Rather sporadic are studies on galls pecked up by birds (Solyom, 2015).

Some authors, e.g. Stille and Dävring (1980), van Meer *et al.* (1995), or Plantard *et al.* (1999) mention the relation between parthenogenetic vermiration (thelytokia) and infection by the bacteria from the family of *Wolbachia* (Hert.) (Rickettsiales) inducing the fusion of infecund female gametes. Kohnen, Wissemann and Brandl (2011) ascertained the common (up to 97%) incidence of infected individuals in the population of *D. rosae*. Kohnen, Richter and Brandl (2012) studied the genetic diversity of *D. rosae* and its common parasitoids *Orthopelma mediator* (Thunb.) (Ichneumonidae) and *Glyphomerus stigma* (F.) (Torymidae). No genetic differences were detected among females from *Rosa canina* L., *R. corymbifera* and *R. rubiginosa* L. (Kohnen, Wissemann and Brandl, 2011). Czeczuga, Czeczuga-Semeniuk and Semeniuk (2008) studied qualitative and quantitative differences in the content of carotenoids in galls, leaves and fruits. These

secondary substances may influence the choice of host plants. Only a few publications were focused on the possibilities of protection and defense against *D. rosae* in garden cultures and plantations of *Rosa* spp. (Lüstner, 1931; Gibson, 1935).

MATERIALS AND METHODS

Field surveys were conducted in the near surroundings of the city of Brno mainly in 2015 and 2016. Attention was paid to localities linked with the northern outskirts of Brno and managed by the Training Forest Enterprise Masaryk Forest Křtiny, specifically to the forest districts of Bílovice nad Svitavou and Vranov. Most of the territory consists of the southernmost part of Dražanská vrchovina Upland natural forest region, and in the forest district of Bílovice nad Svitavou partly also the Protected Landscape Area of Moravian Karst. Numerous observations connected with the collection of galls took part in the forest region situated west of Brno, managed by Forest District Brno (Forests of Brno City/Lesy města Brna, a. s.). Occasional visits were made also to forest stands on the eastern margin of Brno belonging to the forest district of Pozořice (LČR, s. p./Forests of the Czech Republic, State Enterprise). The researched area stretches between 49°10' – 49°19' of northern geographical latitude and 16°30' – 16°45' of eastern geographical longitude. Ground surface orography is articulated with altitude above sea-level ranging from 230 to 400 m. Average annual temperature is 7.5 °C, mean annual precipitation amounts to 610 mm and average growing season lasts 160 days.

The main goal of the study was to determine the hitherto little known course of the evolution of individual developmental stages (larvae in particular) of *D. rosae* on the wild growing *R. canina* in the Brno region. In 2015 and 2016, the galls were examined from June to December (March) at regular week intervals. Partial surveys were made also in 2014 and 2017. Each week, 1 to 5 galls were analyzed in the laboratory (Tabs. I and II). First, the diameter of shoots (right under the gall) and gall dimensions before (and after) the removal of stolons were measured. The galls were gradually cut by surgical knife under microscope. Dimensions of cells were measured micrometrically and the number of cells and their contents were recorded. The growth and development of *D. rosae* larvae and the species' inquiline *Periclistus brandtii* (Ratz.) was assessed according to the micrometrically measured cranium width and total body length and width. The complex examination of galls and their contents provided a basis for deducing the course of gall wasp development from oviposition up to emergence of imagos. The effect of mortality factors on cecidogenesis was among other things ascertained according to the average size of cells with the intact and impaired development of *D. rosae*.

RESULTS AND DISCUSSION

Incidence of imagos and vermination

Diplolepis rosae hibernates in galls persisting on shrubs until the next year (possibly even longer). Unlike in most species from the *Diplolepis* spp. group, the galls remain on plants long after the emergence of imagos sometimes (Blommers, 2008). Thus, old (i.e. last year's and even older) galls and new (i.e. current year's) galls may occur simultaneously on the same shrubs. The species survives the winter period at the stage of grown-up larvae (Schröder, 1967) or prepupae (Williams, Shorthouse and Lee, 2003). According to Kieffer (1914), the galls mature in the autumn and imagos hatch from them in the spring. In the Mediterranean region (Sicily), females hatch from March to June (Rizzo and Massa, 2006), in Sweden, as late as at the end of May and in early June (Stille and Dävring, 1980). Imagos of the related species *D. japonica* (Walk.) appear in Japan from April to the beginning of May within a period of three weeks (Yasumatsu and Taketani,

1967). Occurrence of adults in the spring and in early summer is regulated primarily by temperature, which ensures that gall wasp development is synchronized with the development of host plants (Schröder, 1967).

In the Brno region, *D. rosae* hibernates at the stage of grown-up larvae and prepupae. In winter 2015/2016, its galls contained 30% of grown-up larvae (of which 20% without pupal eyes and 10% with pupal eyes) and 70% of prepupae. In the winter period of 2016/2017, the galls contained 53% of grown-up larvae (of which 28% without pupal eyes and 25% with pupal eyes) and 47% of prepupae. In 2016 and 2017, pupae occurred from 15 March to 15 July and from 20 March to 20 July, respectively. Imagos were hatching from April to July, i.e. four months (Tab. III). In the laboratory conditions, imagos from galls brought on 7 April 2015 were hatching from 5 April to 17 May (Fig. 1).

Males are rare in the population of *D. rosae* than females, and this is why the species verminates almost exclusively through parthenogenesis/parthenogenetically. Although

I: Basic data from field surveys: Average size of current year galls of *D. rosae* (including average number and size of cells in the galls)

Months	Weekly controls	*Control sites	Total number of galls	Diameter of shoots (mm)	Average height/width of galls (mm)	Ditto-without outgrowths (mm)	Average number of cells	Average length/width of cells (mm)
June	8.15.22.29.	3/3/1/3	10	1.6	19.2/24.9	11.1/15.1	47.8	0.7/0.5
July	6.13.20.27.	3/4/4/1	9	1.8	24.8/30.8	13.1/19.2	67.7	2.0/1.5
August	3.10.17.24.31.	1/3/2/2/2	10	2.4	30.7/39.0	16.2/24.0	52.8	2.2/1.7
September	7.14.21.28.	3/1/3/2	8	3.4	32.6/44.0	17.8/22.6	53.9	2.9/2.3
October	5.12.19.26.	3/1/3/3	8	3.5	38.5/45.9	19.8/28.6	78.5	3.6/2.9
November	2.9.16.23.30.	1/2/2/3/1	10	3.8	36.1/45.2	22.6/30.5	51.9	3.7/3.0
December	7.14.21.28.	1/1/1/4	8	2.9	30.9/41.8	18.9/29.9	33.0	3.6/2.9
Total/ Average	–	–	63	(2.7)	(30.1/38.4)	(17.0/24.6)	55.5	(2.8/2.2)

*Forest district Bílovice n. Sv., 2 – Forest district Vranov, 3 – Forest district Brno, 4 – Forest district Pozoříce. Brno region, 8 June–28 December 2015

II: Basic data from field surveys: Average size of current year (up to one year old) galls of *D. rosae* (including average number and size of cells in the galls).

Months	Weekly controls	*Control sites	Total number of galls	Diameter of shoots (mm)	Average height/width of galls (mm)	Ditto-without outgrowths (mm)	Average number of cells	Average length/width of cells (mm)
June	30.	1	1	1.1	15.0/24.0	6.0/12.0	28.0	0.7/0.5
July	7.11.15.19.22.	4/3/1/3/4	12	2.8	24.5/32.1	11.0/15.7	38.7	1.4/1.1
August	1.8.15.22.29.	3/3/1/3/3	11	2.4	24.8/35.0	12.6/18.8	34.5	2.4/1.9
September	5.12.19.26.	3/3/4/3	6	3.4	38.3/43.1	19.0/29.0	58.3	3.0/2.3
October	3.10.17.24.31.	3/2/3/3/3	8	2.9	43.5/49.4	25.0/33.0	58.2	3.5/2.8
November	7.14.21.28.	3/1/3/3	6	3.4	49.8/51.7	31.7/35.0	72.0	3.8/3.2
December	5.12.19.26.	1/1/1/2	5	3.3	43.6/48.6	29.0/36.0	69.6	3.8/3.1
January	2.9.16.23.30.	3/2/3/1/3	8	3.2	32.9/41.9	20.3/31.0	46.6	3.5/2.9
February	6.	3	1	5.0	45.0/50.0	35.0/38.0	69.0	3.7/3.2
March	6.	3	2	3.2	39.0/52.5	28.5/40.0	151.5	?
Total/ Average	–	–	60	(3.0)	(34.4/41.5)	(19.7/26.7)	53.5	(3.0/2.4)

Legend: see Tab. I, Brno region, 30 June 2016–6 March 2017

the species is bisexual according to Gauss (1982), its extremely scarce males are of no importance for vermination. The specific type of parthenogenesis in which unfertilized females verminate by means of diploid eggs from which female progeny hatches again (i.e. thelytokia) is according to recent findings induced by infection caused by the symbiotic bacteria from the family of *Wolbachia* Hert. (Rickettsiales) (Shilthuisen and Stouthamer, 1998; Plantard *et al.*, 1999). The authors found the bacteria in all studied populations of *D. rosae* as well as in a considerable proportion of examined individuals from a wider spectrum of European and non-arctic species of *Diplolepis*. This is why for example populations of *D. spinosissima* (Gir.) with individuals without bacteria exhibited higher representation of males than populations with infected individuals. Apparently, the infection by *Wolbachia* plays an essential role in the vermination strategy of these gall wasps.

The very low (usually less than 1%) representation of males (or their absence) in the populations of *D. rosae* is mentioned e.g. by Kieffer (1914), Schröder (1967) and Gauss (1982). Rizzo and Massa (2006) observed about 4.3% of males in Sicily and Askew (1960) found 0–4.2% of males in England. The highest representation of the males of *D. rosae* in Europe (43.1%) was reported from Bulgaria (Todorov *et al.*, 2012). Populations of *D. japonica* (Walk.) in Japan had 3% of males (Yasumatsu and Taketani, 1967).

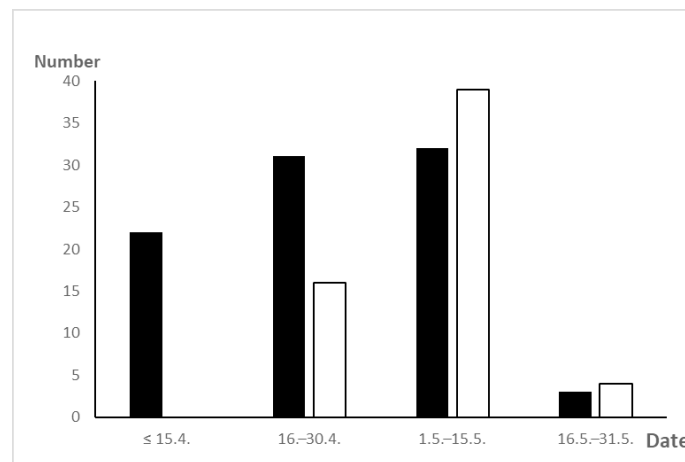
In the Brno region, individuals of both sexes were hatching simultaneously and the share of males in the populations fluctuated from zero to 9% (on average ca. 4.5%).

Soon after their emergence from the galls, imagos search places suitable for oviposition—usually on shrubs on which they developed or on shrubs in the surroundings. Upon finding a properly breaking flower or leaf bud, they tuck the ovipositor among leaflets or flower parts and gradually lay eggs therein. Rarely, they lay eggs also into the shoots just below the buds. Following the oviposition and primarily due to the activity of freshly hatched larvae, galls start to develop on young leaves and/or on petals or sepals of flowers and on fruits.

Young, rapidly growing galls can be found in the open towards the end of May and in early June. Galls developing on leaves are at all times fixed to petiole or midrib, which become swollen due to the presence of eggs and larvae. Blades of effected leaves stop their further growth and become dwarfed. Individual leaflets and their residues often form a conspicuous base of some galls. The galls appear on the adaxial face of leaves first, later also on the abaxial face. In mid-June 2015, numerous galls on the shrubs of *R. canina* in Brno–Černá Pole grew from the adaxial face of 3–10 sepals on relatively well developed fruits (rose hips) of up to 14 mm in height and up to 11 mm in width. This indicates

III: Periods of individual developmental stages/instars of *D. rosae*. Arrow indicates hibernation of a part of the subpopulation of 2nd instar larvae and prepupae. Brno region, 2015–2017

Developmental stages/instars	2015/2016 (from–to)	2016/2017 (from–to)
Eggs	25 May–25 July	5 June–30 July
1 st instar larvae	1 June–31 August	10 June–5 September
2 nd instar larvae	1 July–20 May	1 July–25 May
2 nd instar larvae (pupal eyes)	5 October–30 May	5 October–30 May
Prepupae	12 October–10 June	10 October–15 June
Pupae	15 March–15 July	20 March–20 July
Imagos	1 April–30 July	10 April–25 July



1: Emergence of imagos of *Diplolepis rosae* (dark) and *Periclistus brandtii* (light) from galls brought to laboratory on 7 April 2015

that females laid eggs at up to 10 places from which individual galls were developing, which grew together into composite galls at the base, in whose centre (and/or at the base) fruits (rose hips) were situated. Partial galls could be separated from one another only with difficulties.

The galls of *D. rosae* usually consist of multiple cells. Being more or less grown together, their individual compact parts (with variable numbers of cells) optically represent a single gall. Detailed analyses revealed that females lay eggs at 1–20 (on average 7.0) places. Galls usually grow from one (max. from 4) buds occurring close to one another at a distance of up to 5 mm. It was found out that the number of partial galls increases with the increasing gall size. Small galls (up to 20 mm) usually consist of a single integral gall. These galls are induced by larvae hatched from eggs laid close to one another into a single, relatively tight space. Individual and common occurrence of galls close to one another is mentioned by Gusev and Rimskij-Korsakov (1953).

The number of laid eggs

Females of *D. rosae* can lay more than 700 eggs (Schröder, 1967). Vårdal, Sahlén and Ronquist (2003) found out that females produce on average 408 eggs. Stille and Dävring (1980) mention average fecundity of about 500 eggs, and according to them, females lay 5–10 eggs per hour in laboratory conditions. László and Tóthmérész (2008) observed that galls without parasitoids and inquilines contain most often 25–30 cells that are inhabited at all times only by a single larva. The variable number of eggs in the galls is documented also by Blair (1951) according to whom 50–100 imagos of *D. rosae* hatch from galls without parasitoids.

Galls of *D. rosae* in the Brno region exhibited 5–225 (av. 55.5) cells in 2015 and 1–165 (av. 53.5) cells in 2016 (Tabs. I and II). Thus, at an average number of 500 laid eggs, females could lay eggs on approximately nine different sites under optimal conditions. Nevertheless, the actual number of galls occurring in the open is far from corresponding to the reproduction capacity of females since a great part of laid eggs die and galls are not created. Responsible for the reduced population density of gall wasp are primarily parasitoids, defence reactions of host woody plants and unfavourable weather. Females live for a relatively short time during which they produce several partial clutches by which they induce formation of fewer galls.

Eggs of *D. rosae* are oblong (5 times longer than wide), with long peduncles. Their length is ca. 318 µm, width ca. 59 µm and length of thin peduncle is ca. 917 µm (Vårdal, Sahlén and Ronquist, 2003). They have a colourless, elastic chorion, which allows temporary move of a part of egg content into the peduncle during oviposition. Semipermeable egg membrane provides for chemical communication between the egg and

the host plant tissue, through which the egg volume gradually grows.

Creation of galls

Plants respond to the growth of embryos in eggs and this is why the galls start to be created already at the time when the larvae are still in the eggs (Kieffer, 1914). Statements that are more recent claim that most participating in the creation of galls are freshly emerged egg larvae. The reason is that after hatching, irritants (secrets?) get into adjacent tissues and stimulate them to the fast proliferation (hypertrophy and hyperplasia) of procambial cells. The composition of these metabolites excreted especially by young larvae and showing apparently the nature of growth stimulators is not known yet. Apart from secrets excreted by the larvae, the proliferation of cells is to a lesser extent caused also by the mechanical wounding of cells by fine mouth organs of the larvae etc.

Internal structure of galls was studied e.g. by Shorthouse (1998) or Sliva and Shorthouse (2006). Cells of gall wasps are surrounded by concentrically arranged distinct layers of tissues. The internal layer is formed by nutritive cells, which represent the only source of feed for the larvae. During consumption, these cells are substituted by those from the outer (centrifugally located) intact layer of cells, which is joined to the vascular system of the plant. Characteristic for the histological structure of the galls of *D. rosae* is a continuous transition of the food cell layer into the parenchyma layer and absence of hard (“protective”) cell layer, which is in the galls of many other gallfly species built of thick-walled lignified cells. Thus, the internal tissues of the galls of *D. rosae* are rather homogeneous from the trophic layer up to the epidermis. Young (current year's) galls always contain more water than the adjacent plant tissues.

The surface of the galls of *D. rosae* is covered with numerous moss-like branched outgrowths, which are sticky, soft and elastic at the time of gall growth while old outgrowths are non-sticky, hard and fragile. On the growing galls, they are pea-green, yellow-green and often red on ends (rarely whole). Rusty brown up to red are as a rule only distal (apical) parts of the outgrowths while their bases are green. The colour of galls however tells nothing about their age because even very young galls are often red and grown-up galls are frequently green. On dying and dead galls, the outgrowths turn rusty, brown and black. The shape of galls is globular, oval up to irregularly gnarled with a diameter ranging from 5 to 50 mm (Gusev and Rimskij-Korsakov, 1953; Miller, 1956). According to Nienhaus, Butin and Böhmer (1992), the galls are 4–5 cm large, according to Sedlag *et al.* (1986), their size is approximately as a baby fist, according to Kieffer (1914), Escherich (1942), Schimitschek (1944) and Kovalev (1981) about like a fist.

From the apically narrowing long and mildly warped outgrowths, numerous short (and often

wavy) pointed branches shoot laterally. Outgrowths on the apical part and on the sides of galls are as a rule longer and branched while basal outgrowths are at all times shorter and often non-branched. A gall of average size (height 28 mm and width 37 mm), localized on the apical part of rose hip sized 9 mm in both height and width) was only 15 mm high and 23 mm wide after the removal of outgrowths. There were 697 outgrowths on the gall, whose length ranged from 3 to 22 mm (av. 13.1 mm). From this total number of outgrowths, 50 (7.3 %) were shorter than 5 mm, 89 (12.8 %) were 5–10 mm long, 298 (42.7%) were 10–15 mm long and 260 (37.3%) were longer than 15 mm. An above-average long outgrowth of 17 mm exhibited 55 lateral outgrowths that were 0.5–4.0 mm long and 0.1–0.25 mm wide (at the base). Outgrowths on the gall base were very short (up to 10 mm) and wide 0.2–1.1 mm (av. 0.36 mm) at the base. A very tiny leaf gall of 6 mm in both length and width featured only 50 small (usually non-branched) outgrowths.

The galls of *D. rosae* usually consist of several parts differing in size. Dense fimbriated outgrowths connect these partial segments, giving the galls a monolithic (compact) shape and mossy appearance. Even completely self-contained galls localized close to one another (on 2–4 neighbouring buds) are optically aggregated into a single voluminous gall by means of outgrowths. In Czech, the galls are commonly called as “růžová houba” (bedeguar). In Russian they are called “bedeguar”, in German they are known as Rosenapfel, Rosenschwamm, Schlafapfel and “Bedeguar”, in English as mossy rose gall, rose bedeguar gall (obsolete name is robin’s pincushion) and in French “bédéguar”. The striking appearance of the galls reflected also into the names in many other national languages.

In the Brno region, the galls of *D. rosae* appear earliest at the end of May and in early June; during June and July, they grow intensively. Their size increases during the growing period and the growth ends only as late as in October. In 2015, grown-up galls were on average 35.2 mm high (20.6 mm without outgrowths) and 44.4 (29.7) mm wide. In the climatically more favourable year 2016, the galls

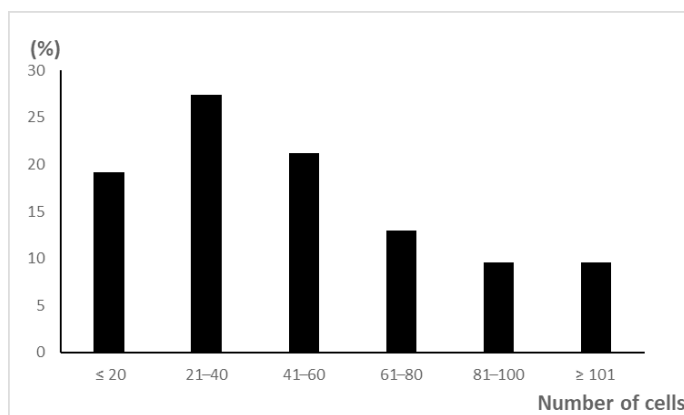
were much larger—on average 45.5 mm (without outgrowths 28.2 mm) high and 49.9 (34.4) mm wide (Tabs. I and II). The smallest galls with 1–2 cells were 10 mm (without outgrowths 4 mm) high and 17 mm (without outgrowths 6 mm) wide. The largest gall with 225 cells was 75 mm (without outgrowths 55 mm) high and 85 mm (without outgrowths 70 mm) wide. The average number of cells in the galls amounted to 52.3 and the highest number of galls (27.4%) contained 21–40 cells (Fig. 2).

Galls of *D. rosae* gain size even when the leaves are fully grown-up (Kieffer, 1914). Their final size depends on the continual feeding of larvae (Redfern, 1997). They persist on woody plants during winter and during the following year, sometimes even longer. Their tissues become darker and lignified. The general appearance of the galls and to a considerable extent also their size and shape alter due to age, climatic impacts and biotic factors. The originally fine pastel coloured “mossy” cover of the galls turns darker and even black; the fragile outgrowths flatten and often crumble down. The gall “body” becomes partly exposed and often features visible craters made by birds, rarely by small rodents.

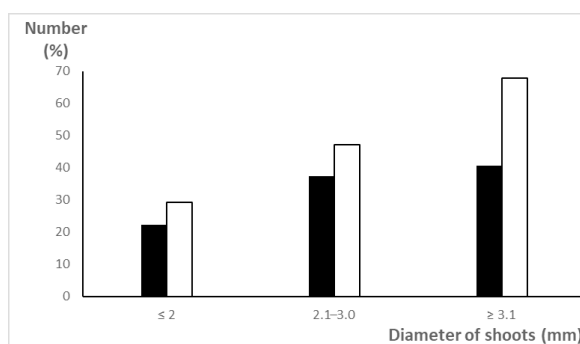
Localization and size differentiation of galls

Galls of *D. rosae* are created only on young and vital annual shoots of *Rosa* spp. In the Brno region, a majority of galls (63.5%) was localized on shoot sides (of which 35.3% on a smaller or larger part of shoot girth and 28.2% everywhere around the shoot). Smaller galls were situated on the shoots usually on one side while large galls (consisting of several more or less elements) encircled the shoot all around. More than a third of galls (36.5%) occurred on the apical growing point or in its close vicinity. While pleurocecidia usually only suppress the growth of shoots, acrocecidia usually terminate their length growth.

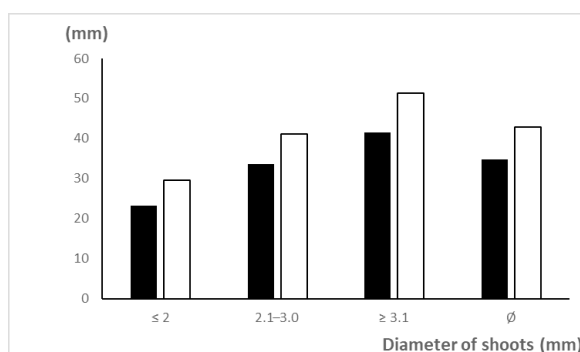
As a rule (85.1%), the gall wasp infested breaking or freshly broken leaves. Far fewer galls (14.9%) were found on flowers and fruits (rose hips). A possibility of the formation of galls from multiple buds can be documented by rather abundant findings of



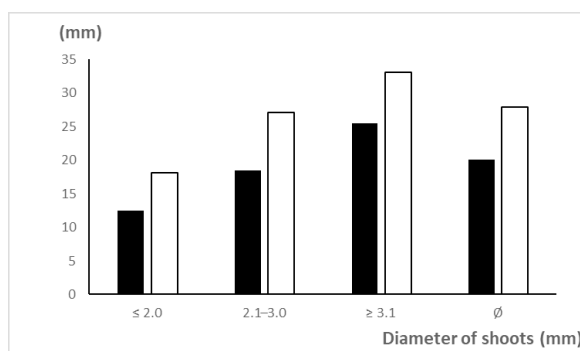
2: Number of cells in the galls of *D. rosae* (in % from the total number of galls). Brno region, June–December 2015, 2016



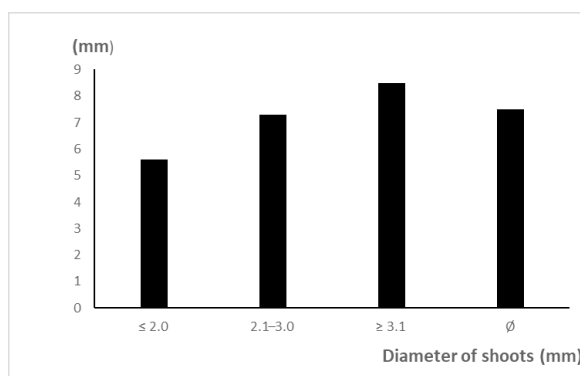
3: Relation between the diameter of grown-up annual shoots of *Rosa canina* and the relative numerical representation of galls of *D. rosae* (dark); Relation between the diameter of shoots and the number of cells in the galls (light); Brno region, 2015, 2016



4: Relation between the diameter of grown-up annual shoots and the average gall height (dark) and width (light); Brno region, September–December 2015, 2016



5: Relation between the diameter of grown-up annual shoots and the average gall height (dark) and width (light) after removal of the outgrowths; Brno region, September–December 2015, 2016



6: Dependence of the average length of outgrowths on the diameter of grown-up annual shoots; Brno region, September - December 2015, 2016

galls with 1–3 normally developed fruits that were partly or completely hidden in the galls. Rarely, galls were created directly on the shoots, at all times in the immediate vicinity of bud bases.

Females of *D. rosae* are highly selective in choosing plants suitable for oviposition. This is among other things documented by the repeated infestation of the same shrubs and a great variability in the number of laid eggs in individual clutches. The number of eggs in the clutch is doubtlessly affected by the vitality of woody plants and related growth rate, by the size and stage of bud flushing, localization of buds on the shrubs etc. The species settles down primarily on the wild *R. canina*, to a lesser extent on other wild growing rose species or rose species escaped from cultivation and rarely on cultivated rose species. Galls can be commonly found on shrubs in forest steppes, in open broadleaved woods, on forest rides and margins, balks, along communications and on various bushy sites. According to Schröder (1967), the galls are more abundant on exposed sites with the annual precipitation below 762 mm and temperature reaching up to 60–80 °F (15.6–26.7 °C).

The size of *D. rosae* galls (without inquiline) is in a positive correlation with the number of cells (László and Tóthmérész, 2013b). The relation

between the gall size and the number of emerged gall wasps is impaired by inquiline, which also have some importance in shaping the structure of gall communities (László and Tóthmérész, 2006). However, the differentiation of gall size does not depend on parasitisation and mortality of gall-forming insects (László and Tóthmérész, 2008). With the increasing size of galls, the percentage of parasitisation decreases and the proportion of emerged progeny is increasing (Ferrari *et al.*, 1997; László and Tóthmérész, 2008). The survival of *D. rosae* increases with the increasing size of galls and decreases with the increasing distance of galls from the ground (László, 2001). The abundance of galls decreases also with the increasing density of shrubs (László and Tóthmérész, 2011). It is stated that the gall wasp infests primarily shrubs stressed by drought, deficiency of nutrients, pruning and the like. It is however not known whether the vitality of shrubs impairs oviposition or whether it suppresses creation of galls. According to the prevailing opinion, young and stressed woody plants tend to produce larger and more abundant galls than old and intact woody plants.

Detailed surveys conducted in the Brno region in 2015–2017 revealed that both the absolute

IV: Head (cranium) width and length/width of vital 1st and 2nd instar larvae of *D. rosae* (1 division = 0.0357 mm). Average cranium width of 1st instar larvae was 7.8 divisions (of which 7.1 and 9.8 divisions in young and growing up larvae, resp.). Average cranium width of 2nd instar larvae was 15.3 divisions (of which 15.1 and 15.4 divisions in young and growing up larvae, resp.). Brno region, 8 June–28 December 2015 and 30 June–6 February 2017

Cranium width (div.)	Living larvae			Average length of larvae (div.)			Average width of larvae (div.)		
	Total	Young	Growing up	Total	Young	Growing up	Total	Young	Growing up
4	8	5	–	16.2	18.0	–	5.8	5.6	–
5	19	10	–	14.1	13.1	–	6.8	7.0	–
6	61	27	1	14.1	13.9	30.0	7.9	7.7	13.0
7	50	12	3	15.7	15.3	32.3	9.2	8.5	14.0
8	42	20	7	16.5	15.9	19.4	10.3	10.2	10.9
9	33	7	9	19.3	18.0	20.9	11.5	10.3	12.9
10	35	5	26	24.1	19.4	26.5	13.5	11.4	15.4
11	26	5	14	25.0	22.2	24.1	13.9	13.2	13.6
12	3	1	4	26.7	32.0	30.5	14.6	16.0	16.3
Total/Average	277	92	64	17.9	15.9	25.0	10.1	9.0	14.1
Average (mm)	–	–	–	0.64	0.57	0.89	0.36	0.32	0.50
12	14	3	5	49.2	32.3	76.4	24.4	16.0	31.8
13	69	18	18	59.1	45.7	77.5	27.0	21.0	35.0
14	168	44	55	68.0	46.7	94.7	29.5	21.9	39.3
15	429	65	210	87.0	56.9	104.4	36.2	25.0	42.1
16	388	45	185	97.8	65.2	112.0	39.1	28.3	43.5
17	143	21	51	87.2	63.2	105.0	38.1	29.3	42.1
18	33	4	7	86.1	65.0	105.7	38.1	35.7	38.6
19	2	1	–	90.0	40.0	–	42.5	25.0	–
Total/Average	1246	201	531	85.8	55.9	104.9	35.8	25.2	41.9
Average (mm)	–	–	–	3.06	2.00	3.74	1.28	0.90	1.50

and the relative representation of galls increases with the increasing diameter of grown-up annual year shoots (measured right below the galls) and the average number of cells in the galls demonstrably increases, too (Fig. 3). Demonstrably increasing with the growing diameter of grown-up annual shoots is also the average size (i.e. height and width) of galls with outgrowths as well as after their removal (Figs. 4, 5) and the average length of outgrowths increases too (Fig. 6). The research showed that the galls of *D. rosae* in the Brno region were most abundant and largest on vital shoots with a high annual increment.

Preimaginal development

Embryonal development of *D. rosae* begins right after oviposition and larvae start hatching from the eggs within a few days. Regarding the long period of oviposition, eggs were found in the Brno region from the end of May or early June up to the end of July, i.e. during the period of two months. Egg larvae emerged within 7–10 days after oviposition. In 2015, larvae of the 1st instar occurred in the period from June to August; in 2016, it was by about a week later (Tab. III). At the beginning of July, larvae of the 2nd instar started to occur in the enlarging cells, which were developing during a greater part of the growing season and came to age in September and October. A part of the grown-up larvae (70% and 47% in 2015 and 2016, resp.) moulted as early as at the end of the growing season and wintered at a stage of prepupa. Larvae emerged from eggs that were laid later came to age too but survived winter in the 2nd instar. The percentage of larvae hibernating in the winter of 2015/2016 and 2026/2017 was 30% and 53%, respectively. The development of *D. rosae* in the galls was apparently accelerated in 2015 by the extremely warm and dry growing season.

Data about the number and development of individual instars of larvae were obtained from the micrometrical measurement of the width of their cranium shell and body (length and width) size (Tab. IV). The table shows among other things that the cranium of the 1st instar larvae is 4–12 divisions (0.14–0.43 mm) wide, and since it is only weakly sclerotised, it can gradually become larger during the growth. The average width of cranium in the 1st instar larvae was 7.8 divisions (0.28 mm); however, the average cranium width of young larvae of this instar was only 7.1 divisions (0.25 mm) and the average cranium width of growing up and grown-up larvae was 9.8 divisions (0.35 mm). This indicates that the cranium width of the 1st instar larvae became larger by 38% during their growth. The larvae of this instar are on average 0.64 mm long and 0.36 mm wide and their body proportions gradually grow in the course of feeding. The increase of average cranium width and body length and width in the 1st instar larvae is apparent from Tab. V.

In the climatically extremely dry and warm growing season of 2015, the 1st instar larvae were on

average smaller (except for cranium) than those in the climatically more favourable year 2016. In 2015, the larvae were on average 0.58 mm long; in 2016, their length was 0.70 mm (i.e. by 20.2% greater). The average width of their cranium in 2015 was 0.30 mm while in 2016 it was 0.26 mm (i.e. by 8.6% narrower). The extremely unfavourable weather of 2015 reflected in the average cranium width increased by 6.9–22.2% (av. 8.6%) and in the average body length decreased by 20.2%. The average width of the body was practically not affected by the extreme weather. The same trends were demonstrated also in the size of young, growing up and grown-up 1st instar larvae.

As opposed to the 1st instar larvae, the cranium of the 2nd instar larvae is more sclerotized and its width hardly increases during the growth (Tab. VI). Cranium width was from 12 to 19 (av. 15.3) divisions, i.e. 0.50–0.68 (av. 0.55) mm (Tab. IV). Average cranium width during feeding increased from 15.1 to 15.4 divisions, i.e. from 0.54 to 0.55 mm (by 1.9%). After moulting, the larvae consume their exuvia, and this is why it was formerly believed they do not moult at all. According to sporadic unverified data, the larvae have allegedly 3–5 instars.

The different weather in 2015 and 2016 had practically no significant influence on the average cranium width. Nevertheless, it had a great impact on the size of larvae. In the extremely warm and dry growing season of 2015, the larvae were on average 2.8 mm long while in the climatically more favourable year 2016, their length was 3.3 mm (i.e. by 15.6% greater). In 2015, the larvae were on average 1.20 mm wide while their width in 2016 was 1.36 mm (i.e. by 13.7% greater). In 2015, the grown-up larvae were on average 3.5 mm long while their length in 2016 was 4.0 mm (i.e. by 14.7% greater). In 2015, the grown-up larvae were 1.38 mm wide while in 2016 their width was 1.62 mm (i.e. by 17.3% greater). Tropical heats and critical drought in the period from 20 June to 31 July 2015 reflected in the growth of larvae which (with the same width of cranium) reached markedly smaller average sizes at the end of the feeding period than in the climatically more favourable year 2016 (Tab. VI).

Cranium width of *D. rosae* and inquiline species *Periclistus brandtii* is illustrated in Fig. 7. The length and width of the larvae of both gall wasp species increase with the increasing cranium width (Figs. 8 and 9). The grown-up larvae of *D. rosae* are yellow unlike the eating larvae, which are whitish. Their body is slightly dorsoventrally flattened, very distinctly segmented, widest at a half of body length or beyond. The end of their body is distinctly elongated (almost like a tail).

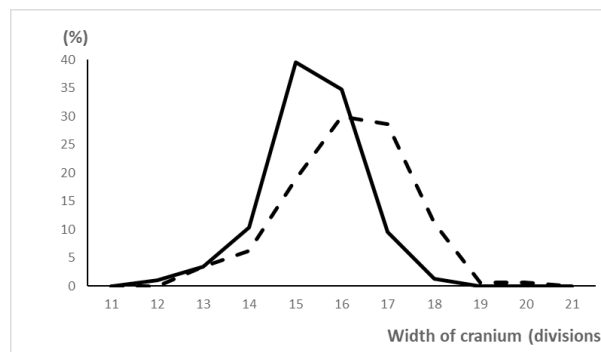
The larvae of *D. rosae* ingest from June to October. Regarding the long period of emergence of imago and oviposition, the actual time of feeding is considerably shorter (ca. 3 months). The first larvae come of age in the 2nd half of August; the last ones come of age in the 2nd half of September and at the beginning of October. The grown-up larvae stop

V: Increase in average cranium width and average body length/width of vital 1st instar larvae of *D. rosae* during feeding (1 division = 0.0357 mm). Brno region, 2015, 2016

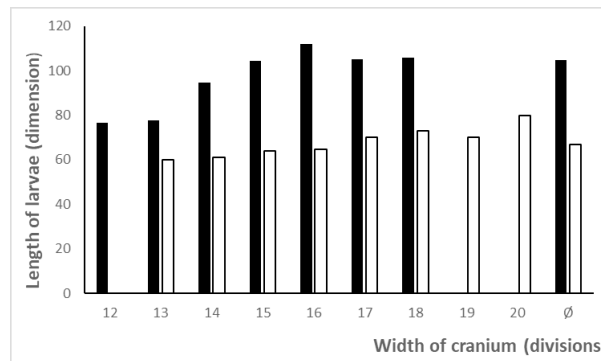
Month	Number of larvae		Average cranium width/body length/body width	
	2015	2016	2015	2016
June	115	15	7.6/14.4/9.1	6.3/15.4/8.7
July	12	98	9.8/25.4/15.1	7.2/19.5/10.1
August	21	10	10.2/19.3/12.4	10.0/23.6/12.4
Total/Average (divisions)	148	123	8.1/16.0/10.1	7.3/19.3/10.1
(mm)	–	–	0.29/0.57/0.36	0.26/0.69/0.36

VI: Average cranium width and average body length/width of vital 2nd instar larvae of *D. rosae* (without pupal eyes) during feeding (1 division = 0.0357 mm). Numbers of larvae examined in 2015 and 2016 were 709 and 566, resp. In the climatically extreme year 2015, the larvae were considerably smaller (with the exception of cranium). Brno region

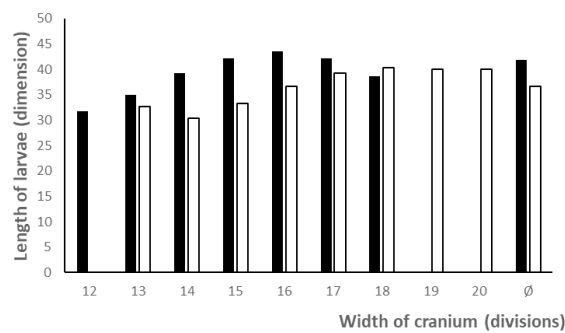
Month	Average cranium width/body length/body width		
	2015	2016	average
July	15.7/66.8/30.1	15.6/70.8/30.6	15.7/68.3/30.3
August	15.2/73.2/31.5	15.0/78.2/31.0	15.1/75.5/31.3
September	15.2/92.0/38.2	15.6/107.9/43.2	15.4/99.5/40.6
October	15.1/88.7/37.7	15.3/117.8/46.0	15.2/104.2/42.1
November	14.5/84.1/33.8	16.4/115.0/45.4	14.8/88.9/35.6
December	16.2/118.8/39.5	15.7/97.4/45.2	16.0/108.8/42.2
Average (divisions)	15.3/81.9/34.2	15.4/93.1/38.0	15.4/87.1/35.9
(mm)	0.55/2.92/1.22	0.55/3.32/1.36	0.55/3.11/1.28



7: Cranium width in the grown-up larvae of *D. rosae* (full line) and *P. brandtii* (hatched line). Cranium of *D. rosae* was wide on average 15.4 divisions; cranium of *P. brandtii* was wide on average 16.1 divisions (1 division = 0.0357 mm). Brno region, 2015–2017



8: Length of the grown-up larvae of *D. rosae* (dark) and *P. brandtii* (light) in dependence on cranium width (1 division = 0.0357 mm). Brno region, 2015–2017



9: Width of the grown-up larvae of *D. rosae* (dark) and *P. brandtii* (light) in dependence on cranium width (1 division = 0.0357 mm). Brno region, 2015–2017

VII: Cranium width of 2nd instar larvae with interlucent compound eyes and their length and width (in dependence on cranium width) (1 division = 0.0357 mm). Average cranium width in 2015 and 2016 was 15.4 divisions (0.55 mm) and 15.6 divisions (0.56 mm), resp. The last two columns show average cranium width of developing prepupae. Brno region, 12 October - 28 December 2015 and 10 October–26 December 2016

Cranium width	Number of larvae		Average body length		Average body width		Average cranium width of prepupae	
	2015/16	total	2015/16	total	2015/16	total	2015/16	total
13	1/1	2	125.0/130.0	127.5	40.0/45.0	42.5	28.0/25.0	26.5
14	10/5	15	134.5/130.0	133.0	47.2/51.8	48.7	31.1/27.6	29.9
15	73/41	114	135.3/138.8	136.6	46.9/50.4	48.2	31.0/29.6	30.5
16	46/46	92	138.3/134.5	136.4	47.1/50.2	48.6	31.4/29.9	30.7
17	7/9	16	130.0/128.9	129.4	43.3/50.0	47.1	28.9/30.6	29.8
18	4/1	5	118.8/100.0	115.0	38.8/50.0	41.0	29.0/36.0	30.4
19	1/-	1	110.0/-	110.0	37.0/-	37.0	27.0/-	27.0
Total/ Average (mm)	142/103	245	135.2/135.1	135.2	46.5/50.3	48.1	30.9/29.7	30.4
	-	-	4.83/4.82	4.83	1.66/1.80	1.72	1.10/1.06	1.08

VIII: Cranium width, body length/width of *D. rosae* prepupae (1 division = 0.0357 mm). In 2015 and 2016, average cranium width was 27.2 divisions (0.97 mm) and 27.7 divisions (0.99 mm), resp. Brno region, 12 October–28 December 2015 and 10 October 2016–6 February 2017

Cranium width	Number		Average length		Average width	
	2015/16	total	2015/16	average	2015/16	average
20	1/1	2	100.0/80.0	90.0	33.0/25.0	29.0
21	1/-	1	100.0/-	100.0	33.0/-	33.0
22	5/4	9	105.0/97.5	101.7	34.2/33.0	33.7
23	7/8	15	105.7/106.3	106.0	35.6/33.9	34.7
24	6/11	17	105.8/102.3	103.5	35.8/34.7	35.1
25	22/23	45	110.7/107.4	109.0	35.7/36.3	36.0
26	24/41	65	112.7/115.2	114.3	37.4/36.8	37.0
27	36/51	87	118.2/120.4	119.5	38.1/38.3	38.2
28	36/67	103	120.1/122.4	121.6	39.4/38.7	38.9
29	24/62	86	121.3/126.0	124.7	39.5/39.8	39.7
30	23/48	71	126.7/127.2	127.0	40.9/40.6	40.7
31	3/8	11	130.0/128.8	129.1	42.3/40.3	40.8
32	2/5	7	125.0/127.2	126.6	42.5/40.0	40.7
33	2/-	2	130.0/-	130.0	47.5/-	47.5
34	-	-	-	-	-	-
35	-/1	1	-/120.0	120.0	-/40.0	40.0
Total	192/330	522	117.4/120.3	119.2	38.2/38.4	38.3
(mm)	-	-	4.19/4.29	4.26	1.36/1.37	1.37

eating and their body slightly shortens. On the inner light-brown to brown wall of cells, there is matt brown meconium which later turns black. During the period of ingestion, liquid dejecta accumulate in the digestive tract, which after their single excretion stick to 20–30% of the inner surface of cells.

Larvae hatched from eggs laid earlier started developing pupal eyes on the sides of cranium from 5 October, and the larvae moulted a week later. Average length and width of the 2nd instar larvae with interlucent compound eyes is presented in Tab. VII. Prepupae and grown-up larvae hibernated and further developed only towards the end of winter and at the beginning of the next year. The prepupae exhibited the average cranium width of 0.98 mm, length of 4.26 mm and width of 1.37 mm (Tab. VIII). As compared with the 2nd instar larvae, they were immobile, their mouth organs were less distinct as well as their body segmentation, the end of their body was not tapered and their colour was achromatic up to lightly yellow-grey.

Pupae of *D. rosae* appear in the Brno region from mid-March to mid-July. Similarly as in the other cecidogeneous Cynipidae species, the pupal stage lasts only a few days. The pupae have a head wide on average 1.18 mm; their body length and width is on average 4.0 mm and 1.47 mm, resp. Imagos hatch from the beginning of April (possibly from mid-April) to the end of July (Tab. III). Their cranium width is on average 1.12 mm, and their body length and width is 3.80 mm and 1.1 mm, resp. (Tab. IX). An overall review of the average size of individual developmental stages (incl. instars) is presented in Tab. X.

The size of cells

From the oviposition to the occurrence of prepupae, the average size (length and width) of cells with intact development of *D. rosae* increases (Tab. XI). After the end of ingestion, the cells are on average 3.9 mm long and 3.1 mm wide. However, grown-up larvae of the 2nd instar with interlucent pupal eyes are on average 4.83 mm long. In order to fit into the cells, their bodies are ventrally bent halfway through. In 2016 (more favourable for the growth of larvae), the cells were on average larger than in the extremely warm and dry year 2015. In addition to the smaller body size, the unfavourable weather in the growing season of 2015 reflected also in the smaller dimensions of cells.

The largest cells are in galls with the grown-up larvae (Tab. XII). The thickness of cells walls ranges from 0.1 to 0.9 mm (at gall circumference up to 5 mm). In October (i.e. after the end of ingestion), the galls gradually start to turn brown and hard (lignified). Following the lump excretion of dejecta, some larvae moult and then become slightly shorter. Then inconspicuous whitish exuvia appear in the galls apart from the prepupae. On the other hand, the inner walls of cells with the larvae of parasitoids are usually light grey up to lightly

grey-pink with the darker to black residues of killed larvae of hosting gall wasps.

Cells with the impaired development of *D. rosae* and cells of inquiline *Periclistus brandtii* are usually smaller than those with the intact gall wasp development are. Cells with parasitoids were on average by 15.3% shorter and by 16.0% narrower. Cells with the larvae dead due to physiological reasons (namely extreme drought) were on average by 24.3% shorter and by 24.6% narrower. The smallest were the cells of *P. brandtii*, which were on average by 43.6% shorter and 50.6% narrower as compared with the cells of *D. rosae* with the intact development (Tabs. XII and XIII).

Inquiline *Periclistus brandtii* (Ratz.)

Galls of *D. rosae* often become the place of developing inquiline *P. brandtii* (Cynipidae). As the other inquilines associated with galls of the genus of *Diplolepis* spp., this species is classified with the rather abundant monophyletic Synergini tribe (Ronquist, 1999), too. Females lay eggs into developing galls. Hatched larvae live mostly together in the self-contained thin-walled cells in the peripheral gall tissues. They cause proliferation of gall parenchyma to create cells of their own and to differentiate their own nutritive cells (Shorthouse, 1998). In literature, *P. brandtii* is usually taken for a harmless inhabitant of galls. According to Wiebes-Rijks and Shorthouse (1992) and László and Tóthmérész (2006), inquilines enlarge the galls, thus disturbing the positive correlation between the number of galls and the number of *D. rosae* individuals. Galls occupied by inquilines represent a food source for parasitoids, by which they participate in increasing the diversity of communities in the galls of *D. rosae*. According to Blair (1943), *P. brandtii* occurs in the galls of *D. rosae* very frequently and sometimes kills the gall wasp. Nevertheless, its impact on the gall-producer is likely to be very small (Stille, 1984). This statement is in contradiction with the findings of Voukassovitch (1928) in Serbia, who raised only *P. brandtii* from the galls of *D. rosae*. For example, Džanokmen (1978) considers *P. brandtii* a parasitoid of *D. rosae* larvae, too.

In the Brno region, *P. brandtii* emerged 2–3 weeks later than *D. rosae*. Imagos of *P. brandtii* were emerging from galls brought into the laboratory on 7 April 2015 from 21 April to 27 May while imagos of *D. rosae* were emerging from 8 April to 17 May. The imagos differ from those of *D. rosae* conspicuously by their morphology and size. Their cranium is 0.50–0.96 mm (av. 0.80 mm) wide, the average body length and width is 2.39 mm and 0.74 mm, resp. (Figs. 7, 8 and 9, Tab. IX). In the studied region, *P. brandtii* was found in ca. 10% of *D. rosae* galls. This inquiline gall wasp inhabited 0–100 (av. 3.6%) of the total number of cells (Tab. XIII). Exceptionally (e.g. on the Kamenný vrch Hill in Brno-Pisárky), the galls contained only cells occupied by *P. brandtii*, this indicating that the inquiline may occasionally live as a parasite also in the galls of *D. rosae* with multiple cells.

IX: Average cranium width and average length and width of imagos of *D. rosae* and *Periclistus brandtii* (1 division = 0.0357 mm). Brno Region, 2015

Cranium width	<i>D. rosae</i>		<i>P. brandtii</i>	
	number	average length/width	number	average length/width
15	–	–	1	40.0/13.0
16	–	–	–	–
17	–	–	3	55.0/15.0
18	–	–	2	55.0/16.0
19	–	–	5	55.0/16.2
20	–	–	13	56.0/17.8
21	–	–	11	62.3/18.7
22	1	80.0/23.0	13	61.5/19.7
23	4	70.5/22.5	17	67.9/21.3
24	3	76.7/21.7	20	74.2/23.1
25	1	80.0/26.0	17	78.5/23.2
26	5	84.0/24.2	6	73.3/24.2
27	7	87.9/26.1	1	82.0/23.0
28	9	89.4/27.0	–	–
29	5	97.0/28.4	–	–
30	25	101.3/28.4	–	–
31	20	103.5/30.8	–	–
32	30	104.2/30.4	–	–
33	27	114.3/33.1	–	–
34	32	121.1/33.8	–	–
35	19	119.5/35.0	–	–
36	2	112.5/31.5	–	–
37	2	132.5/39.0	–	–
Total	192	–	109	–
Average	31.5	106.5/30.8	22.5	67.0/20.7
(mm)	1.12	3.80/1.10	0.80	2.39/0.74

X: Average size of individual developmental stages/instars of *D. rosae* (1 division = 0.0357 mm). Brno region, 2015, 2016

Stage/instar	Average cranium width	Average length	Average width
Eggs	–	7.0	6.5
1 st instar larvae (total)	7.8	17.9	10.1
– young larvae	7.1	15.9	9.0
– growing/grown-up larvae	9.8	25.0	14.1
2 nd instar larvae (total)	15.3	85.8	35.8
– young larvae	15.1	55.9	25.2
– growing/grown-up larvae	15.4	104.9	41.9
2 nd instar larvae (with eyes)	15.5	135.2	48.1
Prepupae	27.5	119.2	27.5
Pupae	33.0	112.3	41.3
Imagos	31.5	106.5	30.8

Mortality

The galls of *D. rosae* provide to their creators favourable environment, i.e. food and protection from adverse climatic effects such as solar radiation and drying out. However, they protect them only partly against insect parasitoids and various predators. Namely the dense branched outgrowths, which are covered with colourless tacky secretion at the time of the growth of galls, have a protective function. The limited protective effect of the mossy cover of the galls is among other things documented also by the fact that only a few small parasitoid representatives of the order of Hymenoptera are trapped and killed thereby.

According to László and Tóthmérész (2011), only 25% of imagos of cecidogeneus *D. rosae* emerge from the galls. The remaining 75% are parasitoids (46%) and inquiline with their own parasitoids (29%). Schröder (1967), Stille (1984) and other authors

specified the composition of insect community associated to the galls of *D. rosae*. The parasitisation ranges from 12.5 to 100% (Rizzo and Massa, 2006). The community of parasitoids and inquiline bound to the galls of *D. rosae* is relatively well known and similar as in other *Diplolepis* spp. (Askew *et al.*, 2006). Its species structure is relatively constant from Spain up to central and Eastern Europe (László, 2001).

From a wide range (ca. 30 species) of parasitoids from the order of Hymenoptera, most frequently mentioned in Europe are *Orthopelma mediator* (Thunb.) (Ichneumonidae), *Torymus bedeguaris* (L.), *Glyphomerus stigma* (F.) (Torymidae), *Eurytoma rosae* Nees (Eurytomidae) and *Pteromalus bedeguaris* (Thoms.) (Pteromalidae). All these species belong to common inhabitants of the galls of *D. rosae* in the Brno region. According to Noyes (2011), *P. bedeguaris* may also infest *O. mediator*, *T. bedeguaris*, *G. stigma*, inquiline *P. brandtii* and the larvae of other *Diplolepis* spp. One of common parasitoids of *P. brandtii* is also *E. rosae* (Rizzo

XI: Increase in average length and width of cells with intact development of *D. rosae* (1 division = 0.0357 mm). Brno region, 2015, 2016

Stage/instar	Number		Average length		Average width	
	2015/16	total	2015/16	average	2015/16	average
Eggs	12/12	24	7.0/7.0	7.0	6.5/6.5	6.5
1 st instar larvae	75/33	108	17.4/16.9	17.2	13.2/13.3	13.2
2 nd instar larvae	290/210	500	72.2/81.3	76.0	58.3/65.0	61.1
2 nd instar larvae–grown-up	98/80	178	105.0/107.8	106.3	84.3/85.4	84.8
2 nd instar larvae–with eyes	91/65	156	106.2/113.3	109.2	86.0/88.7	87.1
Prepupae	101/131	232	106.6/109.0	108.0	85.5/89.7	87.9
Total/average	667/531	1 198	–	–	–	–

XII: Average length and width of cells with intact and impaired development of *D. rosae* (1 division = 0.0357 mm). Brno region, October–December 2015, 2016

Health condition	Number of cells		Average length of cells		Average width of cells	
	2015/16	celkem	2015/16	průměr	2015/16	průměr
Intact development	401/392	793	107.2/110.0	108.6	86.7/89.2	87.9
Parasitoids	84/133	217	87.7/94.7	92.0	70.9/75.7	73.8
Natural mortality	45/61	106	87.8/78.1	82.2	71.2/62.7	66.3
Inquiline	28/14	42	58.9/66.1	61.3	42.8/44.7	43.4
Predators	–/1	1	–/140.0	140.0	–/90.0	90.0
Total/average	558/601	1 159	100.3/102.4	101.4	80.9/82.5	81.7
(mm)	–	–	3.58/3.66	3.62	2.89/2.95	2.92

XIII: Differences in average length and width of cells with impaired/intact development of *D. rosae* – see also Tab. XII. Brno region, October–December 2015, 2016

Health condition	Number of cells (%)		Average length of cells (%)		Average width of cells (%)	
	2015/16	average	2015/16	average	2015/16	average
Intact development	71.9/65.2	68.4	100.0/100.0	100.0	100.0/100.0	100.0
Parasitoids	15.0/22.1	18.7	–18.2/13.9	–15.3	–18.2/15.1	–16.0
Natural mortality	8.1/10.2	9.2	–18.1/29.0	–24.3	–17.9/29.7	–24.6
Inquiline	5.0/2.3	3.6	–45.1/39.9	–43.6	–50.6/49.9	–50.6
Predators	–/0.2	0.1	+ –/27.3	+28.9	+ –/0.9	+2.4
Total	100.0/100.0	100.0	–	–	–	–

and Massa, 2006). Other species often developing in the galls as parasitoids or hyperparasitoids are *Caenacis inflexa* (Walk.) (Pteromalidae), *Eupelmus urozonus* Dalm. (Eupelmidae) and others (Todorov *et al.*, 2012). Apart from *T. bedeguaris*, *G. stigma*, *E. rosae*, *P. bedeguaris* and *E. urozonus*, natural enemies of *D. rosae* in the southern part of the natural range (Turkey) are also *Megastigmus rosae* Bouček (Torymidae), *Aprostocetus eurytomidae* (Nees) (Eulophidae), *Brachymeria walkeri* Dalla Torre (Chalcididae) and *Cotesia pieridis* (Bouché) (Braconidae) (Bayram, Ülgentürk and Toros, 1998). The galls of *D. rosae* host a number of other species and not all of them are parasitoids of larvae (more rarely of prepupae, pupae and imago) of gall-producers. Some species parasitize on the inquiline *P. brandtii*; others are hyperparasitoids and/or superparasitoids. Most geographically spread species develop in the galls of several gall wasp species and only very few species specialize for a certain specific host (Nikolskaja, 1952; Nikolskaja and Zerova, 1978; Džanokmen, 1978 and others). Some natural enemies (e.g. *T. bedeguaris*) may efficiently control the population of their host (Guo *et al.*, 2013).

In 2015 and 2016, parasitoids occurred in the Brno region in 0–78% (av. 15.0%) and in 0–87.5% (av. 22.1%) of cells, respectively (Tabs. XII and XIII). Spectrum and dominance of individual species were not examined. Surprising is a relatively low total proportion of cells with the larvae of *D. rosae* killed by parasitoids (18.7%) and a high share of cells with the vital larvae (68.4%). Average mortality values presented in the tables relate to October–December 2015 and 2016. During winter and spring, the mortality of *D. rosae* further increased, namely due to the pecking up of the galls by birds, rarely due to small rodents eating out the galls etc. The process of gall pecking up starts usually in the first half of January and culminates towards the end of spring. Pecked up is usually up to 75% (av. 30%) of gall contents. On some sites (e.g. on the Palacký vrch Hill in Brno-Žabovřesky and in Brno-Černá Pole), birds caused damage up to 50% of galls. Critical drought and tropical heat waves during the growing season of 2015 caused local drying out of galls and subsequent dying of larvae in the Pozořice forest district. However, total increase of mortality was not recorded in the Brno region. Taking into account all mortality factors, we can state that in the studied region, *D. rosae* completes successfully its development on average in 50% of cells.

Cavities deserted by emerged *D. rosae*, *P. brandtii* and parasitoids often become inhabited by other insect species (e.g. some representatives of Tenthredinidae, Gryllidae, Chalcidoidea and Ichneumonoidea), which find occasional hideaway or place for their own development therein (Hintze-Podufal and Thiele, 1988). Accidental inhabitants of galls are *Cladius pectinicornis* (Geoffr. in Fourcr.) (Tenthredinidae), *Colpoclypeus florus* (Walk.) (Eulophidae) (Todorov *et al.*, 2012) and *Bethylus cephalotes* (Foerst.) (Bethylidae) (Blair, 1944). In the deserted galls of *D. rosae* in the Brno region, we sometimes found larvae from the family

of Tenthredinidae, Ichneumonidae, cocoons with the eggs and nymphs of Araneida, eggs, larvae and imago of *Leptothorax* Mayr (Formicidae), nymphs and imago of Dermaptera, larvae of Neuroptera and others. Gall tissues were often infested by the parasitic fungus *Phragmidium mucronatum* (Pers.) Schl. (syn. *P. subcorticum*/Schr./Wint.).

Economic Importance

Gall wasp *D. rosae* occurs in Europe primarily on wild *Rosa* spp. On cultivated roses, it was observed only sporadically. In terms of forestry, it is a species of no importance. Nevertheless, with respect to its generally abundant occurrence, extensive natural range, size and prominence of its galls, numerous authors consider the species a pest (Kieffer, 1914; Lüstner, 1931; Dmitriev, 1975; Kovalev, 1981; Bayram, Ülgentürk and Toros, 1998; Herting, undated, and others). Economic losses are recorded e.g. in Canada (Gibson, 1935) and in China (Guo *et al.*, 2013). This is why Shorthouse (2015) warns the rose growers about possible passive spreading of the pest by means of galls over long distances.

The galls of *D. rosae* weaken their host plants physiologically, malforming the shape of their low-diameter shoots and causing their dwarfing or even dieback. While pleurocecidia suppress the growth of shoots, acrocecidia terminate the length growth and often induce branching. Therefore, for example Schröder (1967) and Syrett (1990) consider *D. rosae* a promising potential killer of weed *Rosa rubiginosa* in New Zealand. The successful fight with the wild rabbit, which formerly devastated young plants and shoots of this rose species, led to harmful spreading of the rose and to searching efficient methods of its environment-friendly control. The authors recommend supporting the efficiency of *D. rosae* introduction with other prominent natural under-bark and leaf-eating enemies of the rose.

As a rule, *D. rosae* is however taken for a species rather interesting than harmful because the galls are created most frequently on the leaves by contrast to *D. fructuum* (Rübs.), which for example in Turkey caused serious damage on the fruits (rose hips) (Güçlü *et al.*, 2008). In case of need, it can be best controlled after the end of the growing season by removing the galls and their subsequent burning.

In this context, we cannot leave out of consideration some allegedly curative properties of the galls such as sleep inducing capacity that was attributed to them in the past. To cure insomnia, the galls were placed under sleeping pillow. For their astringent effects, they were used to cure diarrhoea, gastritis and enteritis. They were advised at inflammations of oral mucosa and for elimination of toothache. Powder made of galls blended with honey and applied on the head skin was believed to prevent alopecia. As a supposed cure, the galls were used in veterinary medicine and in the medication of honeybee diseases.

CONCLUSION

Thanks to the noticeable and abundant galls, *Diplolepis rosae* is the most popular representative of the cecidogeneous genus of *Diplolepis* spp. on the *Rosa* spp. The objective of the presented study was to examine the species' hitherto little known preimaginal development and gall creation. The research was conducted from June to December 2015 and 2016 in four forest districts in the surroundings of Brno. Galls sampled at week intervals from *R. canina* were microscopically analyzed in the laboratory. Our findings are as follows:

Diplolepis rosae hibernates in the Brno region at a stage of grown-up larvae and prepupae. In the winter period of 2015/2016 and 2016/2017, 30% (53%) of larvae and 70% (47%) of prepupae hibernated, respectively. The extremely warm and dry growing season of 2015 obviously accelerated the development significantly. In 2016 and 2017, prepupae were pupating from 15 March to 15 July and from 20 March to 20 July, respectively. Imagos were emerging in the period from April to July, i.e. 4 months. Individuals of both sexes were hatching at the same time and the share of males in the populations was 0–9% (av. 4.5%).

At average fecundity of 500 eggs, females can lay egg on nine different sites. However, the actual number of galls is lower than the fitness of females due to the mortality of eggs. The galls begin to show at the end of May and in early June; they consist of 1–225 (av. 54) cells. Small galls (up to 20 mm) are usually compact; larger galls (beyond 20 mm) consist as a rule of 2–20 (av. 7) \pm together grown parts. The parts are also connected by numerous outgrowths, which give the galls mossy appearance. A gall of average size (\varnothing 32 mm) features about 700 outgrowths of 3–22 mm (av. 13.1 mm) in length. At the gall apex and on its sides, the outgrowths are longer and branched; at the gall base, they are short and not branching.

The growth of galls is most vigorous in June and July, and gradually ceases in October. In the extremely warm and dry year 2015, the galls were on average 35.2 mm high and 44.4 mm wide. In the climatically more favourable year 2016, the galls were on average 45.5 mm high and 49.9 mm wide. On average 63.5% of the galls were localized on the sides of shoots and 36.5% on the apex. Flushing or freshly broken leaves were infested in 85.1% while flowers and fruits (rose hips) were infested in 14.9%. The largest and most abundant galls were found on shoots with the highest annual increment.

In the Brno region, eggs were occurring from late May to the end of July; 1st and 2nd instar larvae were occurring from June to August and from the beginning of July to the end of October, resp. Some larvae moulted towards the end of the growing season. Hibernating were 47–70% of prepupae and 30–53% of grown-up larvae in the galls.

The 1st instar larvae had the cranium width ranging from 0.14 to 0.43 mm. During the growth, it became enlarged on average from 0.25 to 0.35 mm (by 38%). In 2015, the grown-up larvae of the 1st instar were by 20.2% shorter and by 8.6% narrower than in 2016. The 2nd instar larvae had the cranium width ranging from 0.50 to 0.68 mm. During the growth, it became enlarged on average from 0.54 to 0.55 mm (by 1.9%). Weather differences had no influence on the width of cranium. In 2015, the average length and width of the larvae was 2.8 mm and 1.2 mm, resp. In 2016, the average length and width of the larvae was 3.3 mm (by 15.6% longer) and 1.36 mm (by 13.7% wider), resp. The tropical heat and drought in the growing season of 2015 reflected in smaller dimensions of the larvae.

After the end of feeding, the cells are on average 3.9 mm long and 3.1 mm wide. In the climatically milder year 2016, the cells were larger than in the abnormal year 2015. As compared with the cells with the intact development of the gall wasp, the cells with parasitoids are on average by 15% smaller and the cells with the gall wasp larvae killed by natural factors (primarily drought) are smaller by 24.5%. The smallest cells (by 43.6% shorter and by 50.6% narrower) are those with the larvae of inquiline *Periclistus brandtii*.

Imagos of *P. brandtii* emerged in the Brno region by 2–3 weeks later than imagos of *D. rosae*. The inquiline occurred on average in 10% of galls in 0–100% (av. 3.6%) of cells. Nonetheless, it participates on the mortality of *D. rosae* only occasionally and at a low extent. In 2015 and 2016, parasitoids occupied 0–78% (av. 15.0%) and 0–87.5% (av. 22.1%) of *D. rosae* cells, respectively. From the first half of January to the end of spring, birds caused damage up to 50% (av. 24%) of galls. Pecked out was at all times only a part (max. 2/3) of the gall contents.

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