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APODERUS CORYLI (L.) – A BIOLOGICALLY LITTLE KNOWN SPECIES OF THE ATTELABIDAE (COLEOPTERA)

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Abstract

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Hazel-leaf roller weevil (*Apoderus coryli* /L./) is a noteworthy species from the perspective of biology and forestry; it belongs to the family Attelabidae. Its occurrence, development and harmfulness were studied in surroundings of Brno city in 2011 and 2012. Imagoes of the first generation and those of not very numerous second generation are observed to winter in the area under study. From the beginning of May to the end of July they occur on the host woody plants (mainly on *Carpinus betulus* and *Corylus avellana*). The males and females consume on average 21 and 33 cm^2 of leaves, respectively. The fertilized females cut into the leaf blade in an original manner, and bite into the main and side leaf veins. They fold the withering part of the blade lengthwise to the adaxial face first, and then forming the folded blade into a short cylindrical roll. In the initial phase of rolling, the females lay up on average 1.0 egg into the leaf rolls on *C. betulus* (1.2 on *C. avellana*). In total, they make around 30 rolls. The larvae emerge on average within 10 days. In the course of 3 to 4 weeks, they pass through two instars only and damage on average 4 cm^2 of leaves. This work describes the occurrence and development of the beetles of the first and second generation. It provides an assessment of the mortality of the individual development stages of *A. coryli* within the rolls. It was demonstrated that rolling of the leaves causes on average 9 times more damage to the trees than maturation feeding of the beetles.[1]

Keywords: *Apoderus coryli*, Attelabidae, occurrence, maturation feeding, leaf rolls, reproduction, mortality, harmfulness

INTRODUCTION

Hazel-leaf roller weevil (*Apoderus coryli*/ Linnaeus, 1758/) is a representative of biologically and visually attractive weevil beetles (superfamily Curculionoidea). Initially, the species used to be classified within the large Curculionidae family, later in the Rhynchitidae family. Currently it is included into the Attelabidae family, which is represented in the territory of the Czech Republic by two more species, namely *Compsapoderus erythropterus* (Gmelin) and *Attelabus nitens* (Scop.). Recently, the taxonomical classification of *A. coryli* into the Attelabidae family has been discussed e.g. by Abbazzi *et al.* (1995), Opanasenko & Legalov (1996), Legalov (2011), Legalov & Shevnin (2007), Fowles (2009), Park *et al.* (2012) etc. From other beetles of the Curculionoidea superfamily the taxonomically unstable families of Rhynchitidae and Attelabidae differ both morphologically (especially by straight antennae) and biologically (by the pronounced instinct of maternal care of the progeny).

Apoderus coryli is noteworthy from the point of view of forestry but the pest is of little economic importance. Prior to oviposition, the female makes a single-sided transversal section in the basal part of the leaf blade, and this stretches from the leaf

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margin through the central leaf vein to some of the side veins on the other half of the leaf. Then she bites out numerous incisions into the protruding central vein and the lateral veins from the abaxial face of the blade. Because of disrupted conductive elements, the blade becomes withered. The female folds the supple blade along its central vein and lays up one or a few eggs into the apical part of the fold. Then she rolls the folded blade into a short cylindrical roll closed on both sides. The finished rolls are hanging sideways on the blade base fixed by a link consisting of the unbitten leaf edge. In the second half of the vegetation period, the rolls fall on the ground. The unrolled bases of the blades remain vital, and they usually fall on the ground just prior to the natural leaf shedding. The larvae feed on the withering, decaying and decayed leaf tissues in the interior parts of the rolls, and they pupate within the rolls too. The development is univoltine, and bivoltine under favourable conditions.

Apoderus coryli is one of the most abundant leaf-rolling weevils in the Czech Republic. This fact had been utilised for detailed studying of its incidence, forming of leaf rolls, development and harmfulness. A prevailing part of field research was conducted in the Brno area, namely in the Training Forest Enterprise Masaryk Forest Křtiny, Forests of the City of Brno (Lesy města Brna, a.s.), and Forests of the Czech Republic (Lesy ČR, s.p.), Forest Administration Bučovice in 2011 and 2012.

Geographical Distribution and Host Woody Species

According to Legalov (2011), *A. coryli* occurs in the boreal and sub-boreal zone of the Palaearctic part of Eurasia. Mazur (2011) mentions its wide area stretching in the mesophilous forests from the Atlantic to the Pacific Ocean. Apparently, the centre of its incidence is Central Europe, from where it is reported most often (Klapálek, 1903; Kuhnt, 1913; Reitter, 1916; Escherich, 1923; Scheerpelz & Winkler, 1930; Brauns, 1964 a. o.). *A. coryli* is also known from the other parts of Europe (Abbazzi *et al*., 1995; Fowles, 2009 a. o.) and from the prevailing part of Asia (Schaufuss, 1916), or from Siberia to East Asia (Lohse, 1981; Legalov, 2011; Legalov & Shevnin, 2007). Roubal (1937–1941) mentions its distribution in Europe, the Caucasus, Siberia and North China. So far it was not found e.g. in Israel (Legalov & Friedman, 2007) and Iran (Legalov *et al*., 2010).

Host tree species of *A. coryli* are various broadleaved trees, and mainly *Corylus avellana* L. (Reitter, 1916; Scheerpelz & Winkler, 1930). Schaufuss (1916), according to whom *A. coryli* damages mainly *Corylus*, less often other broadleaved trees (e.g. *Alnus*, *Salix*, *Betula*, and *Fagus*), specifies its trophic requirements in more detail. According to Francke-Grosmann (1974), the main host is *C. avellana*, incidental hosts are *Alnus*, *Fagus*, *Carpinus*, and *Betula*, according to Escherich (1923) also *Quercus* species. Lohse (1981) mentions a much more frequent occurrence on *Corylus* than on *Alnus* and *Betula*. Kuhnt (1913) classifies it among very abundant species on *Corylus*, *Alnus*, and *Quercus*. A broad spectrum of hosts is named e.g. by Brauns (1964), according to whom the most favourite host is *C. avellana*, less suitable hosts being *Fagus*, *Carpinus*, *Quercus*, and *Populus tremula* (L.), and an almost inappropriate host being *Betula*. Burket (1927), Kôno (1930), and Živojinovič (1948) also refer to the trophic affinity of *A. coryli* to *Quercus*. According to Živojinovič (1948), it allegedly occurs also on *Pyrus*. It is evident from the overview, that *A. coryli* is a broadly polyphagous species. However, some data found in the literature are rather unlikely, and therefore require verification.

Biology and Economic Significance

There is a lot of information on the incidence, leaf rolls, development and harmfulness of *A. coryli* in the entomological literature. The data include basic ecologico-faunistic and basic biological information, usually based on non-systematic partial observations or findings taken over from other authors. A few works deal with the seasonal dynamics of the occurrence and/or with the harmfulness and possible protective and control options (e.g. Pavlenko & Gorbunov, 1985; Holecová, 1993; Gantner, 2001; Gantner & Jaskiewicz, 2002). Detailed publications on the biology of *A. coryli* with the specific manifestation of progeny motherly care are only scarce (Kôno, 1930; Daanje, 1957; Park *et al*., 2012). The work by Rossbach (1961), who dealt with the comparison of the relative brain size of *A. coryli* imagoes with those of the *Deporaus*, *Rhynchites*, and *Attelabus* genera, is noteworthy. The author for a certainty proved the biological relationship of the investigated species with markedly different instincts of maternal care of the progeny.

Because of the frequently abundant incidence of the conspicuous beetles and leaf rolls in vast areas, *A. coryli* is mentioned in a majority of comprehensive forestry-entomological and environmental works (Escherich, 1923; Brauns, 1964; Živojinovič, 1948; Koehler & Schnaider, 1972 a. o.).

MATERIAL AND METHODS

Most of the field investigations were carried out in the forest districts Bílovice n. Sv. and Vranov (TFE Masaryk Forest Křtiny), in the Forest Administration Brno (Lesy města Brna, a. s.), and in the Pozořice Forest District (Forest Administration Bučovice, Lesy ČR, s. p.) in 2011 and 2012. The area of interest is located nearby the north-eastern, northern and western parts of the city of Brno. The greatest attention was focused on broadleaved or mixed stands of the 1st age class at the Hádecká planinka Plateau and in its surroundings (Forest District Bílovice n. Sv.). The territory stretches at an altitude of 350 to 420 m. The average annual temperature there is 7.7 °C, average annual rainfall 620 mm, and the mean vegetation period 160 days.

The field investigations concerned young stands of commercial species (mainly of oak) with admixed self-seeded woody plants (e.g. hornbeam, hazel, birch, poplar, and goat willow). In the forest district of Vranov, the occurrence of *A. coryli* was studied among others in the valley of the Rakovecký potok Stream (in the cadastral area of the municipal part Brno-Ořešín). Partial investigations were performed at several other sites in Moravia.

In 2011, regular weekly checks were made from the middle of the growing season, in 2012 throughout the whole vegetation season. Imagoes of *A. coryli* were acquired by simple collection or by using a sweep net between 10 a.m. and 3 p.m. Leaf rolls were sought after in the stands for the purposes of the following laboratory analyses. I measured the dimensions of the rolls, lengths of transversal sections, widths of undamaged marginal parts of the blades (from which the rolls hang), and the number of intact lateral veins in the links. The content of the roll was ascertained microscopically on its unfolding (the number, stage of development, and health condition of *A. coryli*). Instars were determined micrometrically according to the width of the head capsule. The length, width, and area of the damaged leaf and of the rolled part of the blade were recorded. The numbers of incisions made by females in the main and lateral leaf veins were recorded.

Imagoes hatched from the rolls brought to the laboratory or imagoes acquired in the open were placed into glass dishes of 15 to 20 cm in diameter and 6 to 8 cm in height. The fresh twigs of host plants 10 to 15 cm in length were inserted into the dishes every week. Basal ends of the leafy twigs were placed into small dishes containing water and the orifices of the dishes were closed using paper wool. With such rearing arrangement, the leaves were maintaining the required freshness. The damaged leaf area including the number of laid up eggs and the count and volume of the frass produced were recorded continuously. Following the death of the imagoes, the numbers of unlaid eggs in the ovaries were ascertained by microscopic dissection. We studied the time of development of the individual instars, the size of leaf area damaged by them, and defecation of the larvae.

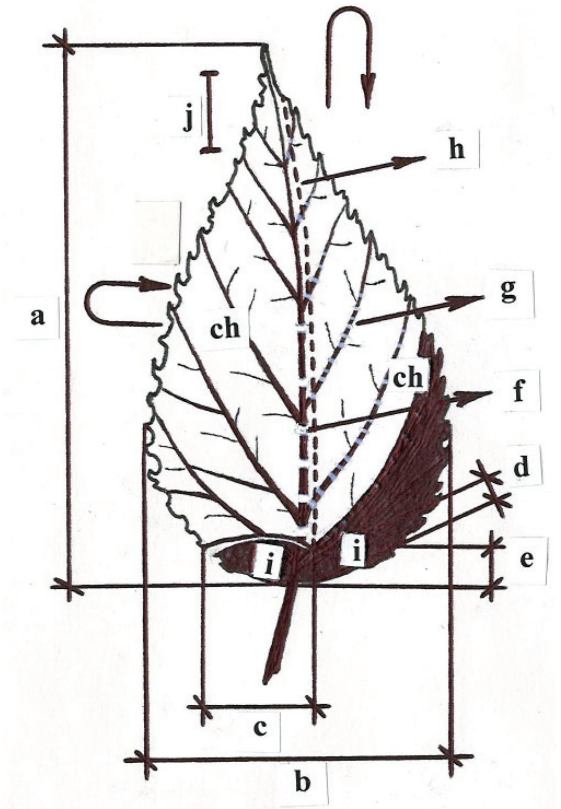
RESULTS AND DISCUSSION

Host Woody Species

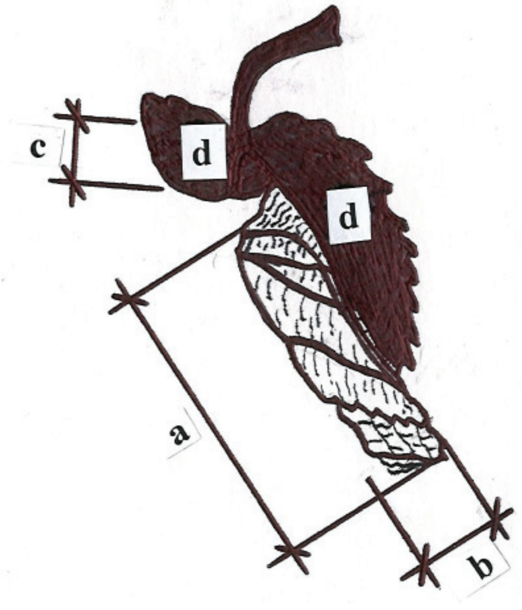
The leaf-rolling weevil *A. coryli* causes damage to woody species by maturation (i.e. maturity and regeneration) feeding of beetles and by making leaf rolls (Figs. 1 to 4). Its development is possible on a number of host species. According to the majority of authors, it is most abundant on *Corylus avellana* L. This fact is reflected

1: *Apoderus coryli*

2: *Feeding notches of the A. coryli imago on the leaf of Carpinus betulus*



3: *Scheme of a C. betulus leaf damaged by an A. coryli female prior to the rolling proper*
Legend: a – leaf length, b – leaf width, c – transversal section, d – undamaged leaf blade part, e – distance of the bite through the central leaf vein from the leaf stalk, f – incisions in the central vein, g – incisions in lateral veins, h – the future longitudinal line of the blade fold, ch – rolled part of the leaf blade, i- unrolled part of the leaf blade, j – oviposition zone



4: *Scheme of an A. coryli roll on the leaf of C. avellana*
Legend: a – length of the roll, b – width of the roll, c – distance of the bite through the central leaf vein from the leaf stalk, d – unrolled part of the leaf blade

in the scientific name of the species as well as in most of vernacular names (e.g. in Czech, Slovak, English, German, Russian, Polish, Spanish etc.). In the Czech language, *A. coryli* was designated as "úzkošíjník lískový" first (Klapálek, 1903). The currently valid Czech name "zobonoska lísková" was adopted in the 1950s. Its host species are often considered to be also those of the genera *Alnus*, *Fagus*, *Betula*, *Quercus* and *Carpinus*, rarely *Salix*, *Populus tremula* L. and *Pyrus*.

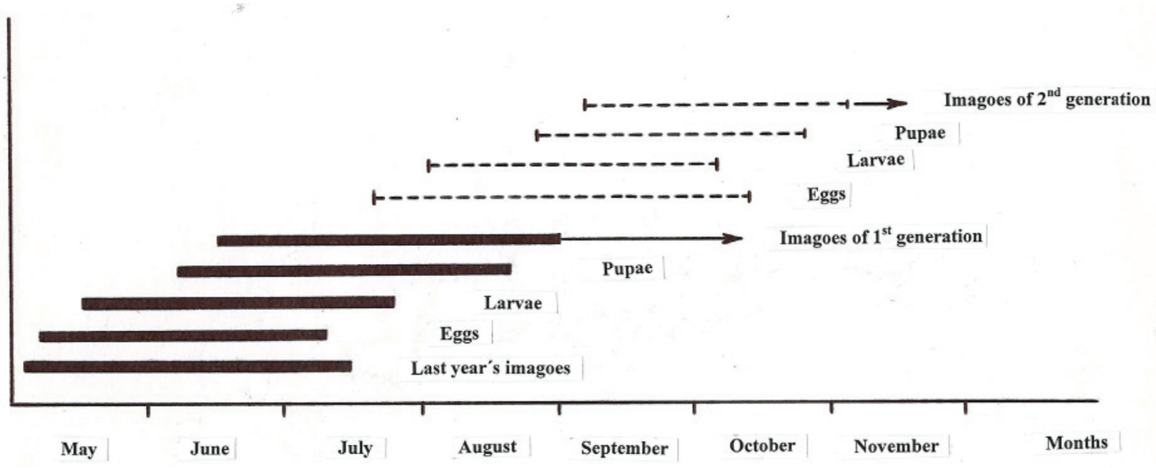
I: *The average size of rolls, damaged leaves, and the average count of Apoderus coryli eggs on Carpinus betulus and Corylus avellana*. The Brno area, 2011.*

Date	Locality (district)	Number of rolls	Average length/width		Total/rolled leaf area (cm^2)	Rolled leaf area (%)	Number of eggs
			of rolls (mm)	of leaves (mm)			
27 July	Bílovice n Sv. (Brno-Province)	8 2*	20.6/7.3 38.0/15.0	75.9/42.9 70.0/66.0	22.1/17.0 37.0/24.0	76.9 64.9	1.0 1.0
30 July	Vranov (Brno-Province)	31 -*	17.7/7.3 -	73.0/39.2 -	19.7/17.3 -	87.8 -	0.8 -
3 Aug.	Bílovice n. Sv. (Brno-Province)	40 15*	17.4/7.0 29.8/10.4	70.5/38.4 71.5/58.7	17.9/15.7 31.1/23.6	87.7 75.9	0.8 1.0
24 Aug.	Bílovice n. Sv. (Brno-Province)	25 3*	16.4/6.6 17.0/7.0	65.2/35.2 46.0/42.0	15.6/13.7 14.0/12.5	87.8 89.3	1.0 1.0
31 Aug.	Bílovice n. Sv. (Brno-Province)	25 5*	16.3/7.0 25.2/9.2	67.9/37.4 64.0/51.6	16.8/14.5 24.6/21.7	86.3 88.2	0.8 1.4
7 Sept.	Bílovice n. Sv. (Brno-Province)	23 7*	16.5/7.0 24.3/9.3	66.6/38.0 67.3/51.2	17.6/15.2 24.8/21.9	86.4 88.3	1.0 0.8
10 Sept.	Bílovice n. Sv. (Brno-Province)	30 21*	18.4/7.2 27.1/9.2	73.3/39.8 69.3/57.5	20.5/18.0 31.0/23.9	87.8 77.1	1.0 1.0
14 Sept.	Bílovice n. Sv. (Brno-Province)	22 3*	17.1/6.7 22.5/8.5	63.2/37.1 61.7/49.7	16.2/13.9 24.3/19.0	85.8 78.2	1.0 1.5
17 Sept.	Vranov (Brno-Province)	78 -*	17.2/6.6 -	63.3/38.9 -	17.4/14.3 -	82.2 -	0.9 -
21 Sept.	Horákov (Brno-Province)	65 13*	17.1/6.5 28.5/8.9	64.7/37.1 72.2/56.6	16.8/14.4 31.8/24.2	85.7 76.1	0.95 1.1
24 Sept.	Podkomorské forests (Brno-City)	48 4*	16.9/6.7 25.7/9.5	65.5/37.4 70.0/56.5	17.1/14.8 29.5/24.2	86.5 82.0	0.95 1.0
28 Sept.	Bílovice n. Sv. (Brno-Province)	30 9*	16.5/6.6 26.2/10.5	62.7/36.4 73.6/60.0	16.0/13.8 33:0/26.3	86.3 79.7	1.0 2.2
5 Oct.	Bílovice n. Sv. (Brno-Province)	19 2*	16.0/6.6 31.0/10.5	65.0/35.6 80.0/69.5	16.0/14.2 44.0/32.5	88.8 73.9	0.85 1.5
12 Oct.	Bílovice n. Sv. (Brno-Province)	26 1*	16.7/6.9 25.0/9.0	69.5/37.5 75.0/60.0	18.0/15.9 39.0/16.0	88.3 41.0	1.0 1.0
15 Oct.	Vranov (Brno-Province)	16. 4*	16.6/6.7 29.0/10.8	62.7/35.5 77.5/64.5	15.0/13.4 38.0/33.6	89.3 88.4	0.7 1.0
19 Oct.	Bílovice n. Sv. (Brno-Province)	12 6*	16.7/6.5 27.0/8.5	65.6/38.9 70.7/60.3	17.1/15.4 31.2/25.7	90.0 82.4	0.8 1.8
23 Oct.	Doubravník (Brno-Province)	17 -*	15.7/6.2 -	61.1/36.4 -	14.7/12.8 -	87.1 -	0.9 -
26 Oct.	Podkomorské forests (Brno-City)	29 6*	16.2/6.7 24.6/8.8	68.9/38.1 66.2/55.5	17.3/15.3 26.3/19.8	88.4 75.3	0.8 1.8
29 Oct.	Vranov (Brno-Province)	12 4*	16.5/6.8 27.2/9.5	69.2/35.8 77.5/62.7	17.3/15.1 33.0/28.2	87.3 85.4	0.8 1.5
2 Nov.	Bílovice n. Sv. (Brno-Province)	14 2*	17.8/6.7 23.5/9.5	69.1/40.7 63.5/56.0	19.6/16.4 25.0/17.0	83.7 68.0	0.9 1.0
9 Nov.	Bílovice n. Sv. (Brno-Province)	10 1*	18.1/7.4 35.0/12.0	69.6/40.7 75.0/66.0	18.3/15.4 38.0/28.0	84.1 73.7	0.9 2.0
Total (average)		580 108*	17.0/6.8 27.0/9.5	66.7/37.8 69.8/57.4	17.4/15.0 30.3/23.8	86.2 78.6	0.9 1.26

In the varied woody species composition in the stands of the 1st age class, all of the potential host woody species of *A. coryli* were represented in the Brno area. The beetles (including maturation feeding and rolls) were found as being most abundant on *Carpinus betulus* L., plentiful on *C. avellana*, and sparse on *Alnus glutinosa* Gaertn. Several times imagoes were observed feeding on *Betula pendula* Roth. In 2011, the rolls on *C. betulus* were 5.4 times (in 2012 3.3 times) more abundant than on *C. avellana* (Tabs. I and II). The high trophic affinity of *A. coryli* to *C. betulus* is not mentioned in the available literature. The absence of leaf rolls on the other woody species (except from *A. glutinosa*) is likewise surprising. For this reason, the trophic attractiveness of woody species for *A. coryli* requires a proper verification also in the other parts of its wide natural range.

II: *The average size of rolls, damaged leaves, and the average count of A. coryli eggs on C. betulus and C. avellana*. The Brno (Vsetín) area, 2012.*

Date	Locality (district)	No. of rolls	Length/width of rolls (mm)	Length/width of leaves (mm)	Total/ rolled leaf area (cm^2)	Rolled leaf area (%)	Number of eggs
6 May	Vranov (Brno-Province)	1 1*	25.0/7.0 22.0/7.0	95.0/55.0 72.0/55.0	35.0/32.5 26.0/22.5	92.9 86.5	1.0 1.0
16 May	Bílovice n. Sv. (Brno-Province)	9. 5*	17.4/6.9 22.5/8.2	70.7/42.7 65.4/50.0	19.9/17.7 23.1/20.6	88.9 89.2	0.8 0.4
23 May	Vranov (Brno-Province)	13 5*	18.4/6.7 28.2/9.8	75.9/41.4 78.6/62.6	21.8/19.6 34.8/30.2	89.9 86.8	1.2 2.0
30 May	Podkomorské forests (Brno-City)	30 5*	16.9/6.4 24.0/8.8	83.9/46.8 75.0/57.4	21.4/19.6 29.0/25.6	91.6 88.3	1.1 1.2
6 June	Vranov (Brno-Province)	36 8*	18.3/6.7 23.9/8.2	71.3/39.4 67.7/57.7	19.0/17.1 29.0/26.9	90.0 92.7	0.9 0.9
13 June	Vranov (Brno-Province)	53 5*	17.3/6.7 26.0/8.7	68.3/38.7 74.3/58.8	17.9/16.4 31.7/-	91.6 -	0.8 1.3
18 June	Valašská Bystřice (Vsetín)	2 23*	15.5/6.5 24.0/8.0	71.0/36.0 74.2/55.4	17.5/15.5 29.8/26.5	88.6 88.9	1.0 0.8
20 June	Vranov (Brno-Province)	55 6*	16.9/6.7 22.2/8.5	67.2/37.7 63.7/48.8	17.1/15.6 22.0/20.4	91.2 92.7	1.0 1.2
27 June	Bílovice n. Sv. (Brno-Province)	30 17*	17.2/6.8 25.0/8.4	63.7/37.7 67.8/53.9	16.7/15.1 25.4/22.8	90.4 89.8	1.0 1.2
4 July	Podkomorské forests (Brno-Province)	30 9*	16.8/6.9 25.7/8.7	66.1/39.4 75.2/57.3	17.2/15.7 30.4/28.1	91.3 92.4	0.9 1.0
11 July	Podkomorské forests (Brno-City)	35 13*	16.5/6.7 26.1/9.4	67.1/37.1 72.0/55.7	17.0/15.7 30.4/28.6	92.3 94.1	1.0 1.2
18 July	Horákov (Brno-Province)	94 16*	15.1/6.5 27.8/9.3	61.0/34.0 77.6/61.4	14.0/13.0 36.1/30.9	92.9 85.6	1.0 1.4
25 July	Podkomorské forests (Brno-City)	63 8*	15.6/6.7 24.7/8.9	65.8/35.9 70.2/57.7	15.8/14.5 29.9/25.9	91.8 86.6	1.2 1.1
1 Aug.	Bílovice n. Sv. (Brno-Province)	37 23*	17.9/7.3 25.0/8.6	70.4/39.9 70.2/56.3	19.0/17.6 28.5/25.7	92.6 90.2	1.0 1.5
8 Aug.	Mariánské valley (Brno-City)	36 50*	17.8/7.3 26.1/9.4	69.8/39.5 71.1/57.9	18.7/17.3 30.1/26.6	92.5 88.4	1.2 1.4
15 Aug.	Doubravník (Brno-Province)	38 20*	17.4/7.0 27.1/9.8	67.8/38.5 73.6/60.6	16.9/15.4 33.5/30.5	91.1 91.0	1.0 1.1
22 Aug.	Tišnov (Brno-Province)	24 34*	16.3/6.5 22.5/8.8	60.9/35.0 67.1/51.6	15.3/14.5 24.3/22.4	94.8 92.2	1.2 1.2
29 Aug.	Horákov (Brno-Province)	80 3*	16.6/7.0 23.5/9.0	63.6/36.9 60.0/46.0	16.3/15.2 23.0/22.2	93.2 96.5	1.1 1.0
5 Sept.	Horákov (Brno-Province)	75 10*	16.1/6.7 25.4/9.1	64.7/36.5 65.8/57.4	15.6/14.0 27.5/24.0	89.7 87.3	1.2 1.5
12 Sept.	Horákov (Brno-Province)	59 10*	15.8/6.8 24.2/9.4	60.3/35.9 74.4/57.9	15.1/13.6 30.9/26.2	90.1 84.8	1.0 1.1
19 Sept.	Bílovice n. Sv. (Brno-Province)	36 8*	15.6/6.5 21.0/8.6	60.8/35.7 69.0/57.0	14.4/13.1 30.4/20.0	91.0 65.8	1.2 1.0
26 Sept.	Horákov (Brno-Province)	47 13*	14.7/6.4 29.2/9.9	56.8/32.9 74.5/62.1	13.0/12.0 31.6/30.6	92.3 96.8	1.1 1.6
3 Oct.	Vranov (Brno-Province)	74 16*	16.0/6.6 24.9/9.9	62.0/35.7 73.7/56.7	15.4/13.8 30.5/27.0	89.6 88.5	1.1 1.2
10 Oct.	Vranov (Brno-Province)	55 -*	16.4/6.8 -	65.4/37.3 -	16.5/14.6 -	88.5 -	1.0 -
17 Oct.	Bílovice n. Sv. (Brno-Province)	15 10*	16.2/6.8 24.0/8.8	63.0/36.5 68.8/56.6	15.9/14.1 29.4/24.8	88.7 84.3	1.1 1.3
24 Oct.	Podkomorské forests (Brno-City)	25 4*	15.2/6.3 30.0/10.2	59.6/33.5 70.0/64.2	14.1/12.7 37.5/32.2	90.1 85.9	1.1 1.5
31 Oct.	Podkomorské forests (Brno-City)	4 -*	16.2/6.7 -	62.2/37.5 -	16.7/14.7 -	88.0 -	0.8 -
Total (average)		1 056 322*	16.4/6.8 25.2/9.0	65.1/37.1 71.1/56.7	16.3/14.9 29.4/26.2	91.4 89.1	1.05 1.24



5: *Basic scheme of the development of A. coryli. The Brno area, 2012.*

The wintering stage

Published data on the development and wintering stages of *A. coryli* are sparse. According to some authors, the mature larvae of the winter in the ground (Burket, 1927; Koehler & Schnaider, 1972; Francke-Grosmann, 1974 a.o.) or in the fallen leaf rolls (Brauns, 1964). On the contrary, Lohse (1981) and some other authors maintain that beetles of the second generation represent the wintering stage.

In the Brno area, mainly the imagoes of the first generation wintered in 2011 and 2012, as well as the imagoes of the not very numerous second generation (Fig. 5). The larvae always pupated at the places of their development (i.e. within the rolls), and the imagoes used to appear in the open nature prior to their departure to wintering grounds.

Incidence of the Beetles on Trees and Their Maturation Feeding

With the oncoming warmer spring weather, the beetles of *A. coryli* leave their wintering hiding places and appear on the host tree species. In the Brno area, they usually colonize woody plants as early as at the beginning of May. The number of imagoes on trees culminates in the second half of May. In mid-July, the beetles gradually die (Fig. 5). Holecová (1993) arrived at a similar finding in Slovakia; she used to find the beetles on hazel mainly in May and in June.

As soon as the beetles reach the host tree species, they begin their maturation feeding immediately. They start to bite out oval holes (windows) of an average 8.6 mm^2 area from the adaxial face of the leaves. On the leaves of hornbeam, the average area of feeding notches was 8.0 mm^2 while on the leaves of hazel the average size of the feeding notches was 9.1 mm^2. The average area of male feeding notches on the leaves of hornbeam (7.6 mm^2) was by 1.6 mm^2 smaller than on the leaves of hazel. The average area of female feeding notches on the leaves of hornbeam (8.5 mm^2) was by 0.5 mm^2 smaller than on the hazel leaves. The beetles make no harm to the main vein or lateral veins, but they do damage vein anastomoses. Denser pattern of lateral veins in hornbeam (i.e. narrower leaf areas among the lateral veins) are apparently the reason for a somewhat smaller area of feeding notches on the leaves of hornbeam (as against hazel). The difference in the average size of feeding notches bitten out into the leaves of hornbeam and hazel by beetles of the new generation prior to their departure into the wintering grounds was even more conclusive. The average area of the feeding notches made by males and females on the leaves of hornbeam and hazel was 5.5 mm^2 and 8.1 mm^2, respectively. On the younger leaves of hazel, the feeding notches were markedly larger than on the older leaves. No difference was observed in the size of feeding notches made by males and by females.

Parent beetles occur on the woody plants for one and a half to two months. They are mainly active in warm and sunny weather, when they also can fly quite well. They utilise their flying faculties primarily for seeking suitable trees in the close and more distant vicinity as well as for intraspecific communication. They are very wary and escape danger by running, falling on the ground, or taking off. The total consumption of leaves by males is on average 21 cm^2 (Tab. III), by females 33 cm^2 (Tab. IV). In selective laboratory tests, around 80% of beetles consumed more leaves of hazel than of hornbeam, and only around 20% of beetles fed more on the leaves of hornbeam than of hazel.

It ensued from a week of laboratory investigation conducted towards the end of May 2012 that during a day (24 hours), beetles kept in connubial couples bit out on average 9.4 feeding notches of an average area of 8.0 mm^2 in hazel, i.e. altogether 75 mm^2 per day. They fed most at night (from 6 p.m. to 6 a.m.), during which time they made on average 6.6 (70.2%) feeding notches (Tab. V). They bit out a feeding notch of below-average size (1 to 5 mm^2) in 1 to

III: *The course of feeding and defecation of A. coryli male. From 8 May, the imago was offered leafy shoots of C. betulus and C. avellana. The male damaged 7.8 cm² (37.5%) and 13.0 cm² (62.5%) of the leaves of C. betulus and C. avellana, respectively. Laboratory research, 2012.*

Date	Damage to the leaves (cm²)	Count of frass	Average length/ width of the frass (mm)	Average volume of one piece of frass (mm³)	Volume of the frass (mm³)
15 May	5.6	302	0.79/0.25	0.0387	11.687
22 May	5.0	298	0.86/0.28	0.0529	15.764
29 May	4.4	241	0.82/0.26	0.0435	10.483
5 June	3.7	162	0.85/0.26	0.0451	7.306
12 June	1.1	60	0.96/0.27	0.0549	3.294
19 June	1.0	42	0.89/0.29	0.0587	2.465
Total (average)	20.8	1 105	0.84/0.264	0.0461	50.999

IV: *The course of feeding, oviposition and defecation of two A. coryli females (A, B). From 8 May 8, the imagoes were offered leafy shoots of C. betulus a C. avellana. Female A damaged 5.6 cm² (18.4%) of the C. betulus leaves and 24.8 cm² (81.6%) of the C. avellana leaves. Female B damaged 13.4 cm² (38.1%) of the C. betulus leaves and 21.8 cm² (61.9%) of the C. avellana leaves. In the ovaries of the dead females A and B, there were five and one unlaid eggs, respectively. Laboratory research, 2012.*

Date	Damage A/B (cm²)	Number of eggs A/B	Number of frass A/B	Average length×width of the frass A/B (mm²)	Average volume of one piece of frass A/B (mm³)	Volume of the frass A/B (mm³)
15 May	6.2/7.4	7/6	310/277	0.89 × 0.26/0.89 × 0.26	0.0472/0.0472	14.632/13.074
22 May	7.3/6.3	6/4	318/268	0.89 × 0.36/0.96 × 0.34	0.0905/0.0871	28.779/23.343
29 May	2.3/3.1	5/4	102/137	0.93 × 0.32/0.96 × 0.32	0.0748/0.0772	7.630/10.576
5 June	4.1/5.6	3/2	153/238	1.00 × 0.29/0.89 × 0.30	0.0660/0.0629	10.098/14.970
12 June	1.8/4.9	3/1	107/172	1.03 × 0.30/0.96 × 0.30	0.0728/0.0678	7.790/11.662
19 June	6.9/5.3	1/2	344/276	0.93 × 0.31/1.03 × 0.32	0.0702/0.0828	24.149/22.853
26 June	1.8/2.6	-	104/138	0.96 × 0.29/0.96 × 0.29	0.0634/0.0634	6.594/8.749
28 June	-	-	-	-	-	-
Total (average)	30.4/35.2	25/19	1 438/1 506	0.93×0.31/0.95×0.31	0.0693/0.0700	99.672/105.227

2 minutes, an average-sized feeding notch (6 to 10 mm²) in 3 to 5 minutes, and an above-average sized notch (11 to 15 mm²) in 6 to 8 minutes.

After 1 to 3 days of food intake, the beetles mate for the first time. In the open, the copulating beetles can be encountered most frequently in May and less often in June. In the laboratory conditions, the beetles mated on average 3.3 times a day for the period of approximately 50 minutes. During 24 hours, they copulated on average 2 hours and 45 minutes. Most often (2.8 times), they copulated during the light part of the day (from 6 a.m. to 6 p.m.) (Tab. V). The most intense copulation was observed around midday (from 10 a.m. to 2 p.m.). The males often (up to 6 times a day) climbed on the females attempting to mate with them. These unsuccessful attempts of the males at copulation lasted on average 30 minutes, i.e. a substantially shorter time than actual copulation. Subsequently the fertilized females started to make leaf rolls and lay eggs thereinto.

Leaf Rolling

Sexually mature and inseminated *A. coryli* females seek for leaves of suitable size, shape and consistency for the oviposition on young, freshly flushed host woody plants. From the adaxial face of the selected leaves, the females make cuts near the leaf bases, creating a single-sided, transversal section. From the left or right margin of the blade, this bow-shaped section stretches to the opposite edge of the blade. The section usually intersects two lateral veins vertically first, then the central vein and finally one (scarcely two) lateral veins on the other half of the blade, where it is terminated a few mm in front of the leaf margin.

V: *Feeding and copulation of A. coryli during the day (24 hours). Two pairs of the last year's imagoes were evaluated independently on the leaves of C. avellana. The average area of feeding notches was 8 mm². Laboratory research, 24–30 May 2012.*

Period of the day (from–to)	Average number of feeding notches	Average damaged leaf area (mm²/%)	Average count of copulations	Average time of one copulation (min)	Total time of one copulation (min./%)
0–6	2.9	23.2/30.8	0.2	30	6/3.6
6–12	1.3	10.4/13.8	1.5	59	89/54.0
12–18	1.5	12.0/16.0	1.3	40	52/31.5
18–24	3.7	29.6/39.0	0.3	60	18/10.9
Total (average)	9.4	75.2/100.0	3.3	50	165/100.0

VI: *Basic characteristic of A. coryli leaf rolls on C. betulus (in the numerator) and C. avellana (in the denominator) depending on the area of damaged leaves. Presented are total and mean values. The Brno (Vsetín) area 2011, 2012.*

Characteristics	Area of the damaged leaves of *C. betulus/C. avellana* (cm²)			
	≤ 13/ ≤ 25	14–18/ 26–35	≥ 19/ ≥ 36	Total
Number of rolls	474/145	606/163	477/105	1 557/413
Area of the damaged leaves (cm²)	11.3/20.1	16.0/30.1	22.8/43.0	16.6/29.7
Area of the rolled parts of leaves (cm²)	10.2/17.9	14.3/26.2	20.1/36.5	14.9/25.6
Area of the unrolled parts of leaves (cm²)	1.1/2.2	1.7/3.9	2.7/6.5	1.7/4.1
Percentage of the unrolled parts of leaves (%)	9.7/10.9	10.6/13.0	11.8/15.1	10.2/13.8
Length of the rolls (mm)	14.1/21.5	16.3/26.1	19.5/31.0	16.6/25.7
Width of the rolls (mm)	6.1/8.3	6.7/9.3	7.4/10.5	6.7/9.2
Length of the transversal sections (mm)	11.7/15.2	13.1/17.6	14.9/20.3	13.2/17.4
Sections from left (%) (complement to 100% = incisions from the right)	47.9/45.6	47.5/44.5	49.6/42.1	48.2/44.3
Length of the slight tears on blades (mm)	1.7/2.2	1.9/2.7	1.9/3.0	1.9/2.6
Width of the links of blade basal parts with the rolls (mm)	5.3/7.1	6.1/8.5	7.1/10.3	6.2/8.5
Number of lateral leaf veins in the links	2.0/1.6	2.1/1.6	2.1/1.6	2.1/1.6
Distance of bites in central veins from leaf stalks (mm)	6.7/4.4	7.8/5.5	8.7/5.6	7.7/4.9
Number of incisions in central veins	5.6/5.7	6.3/6.1	7.1/6.7	6.3/6.2
Number of incisions in lateral veins	40.0/40.3	44.2/47.7	47.7/41.1	44.1/43.6
Number of eggs in the rolls	1.00/1.16	1.02/1.16	0.95/1.45	0.99/1.22
Order of the rolls from terminal buds	3.2/1.7	3.5/2.2	4.0/2.8	3.5/2.2

Both parts of the partly cut blade are connected by the untouched margin of the leaf reinforced by one (at the most two) lateral veins. Various deviations scarcely occur from this kind of the preparation of leaves for rolling. For instance, a female cuts into the leaf blade from both sides, but she causes no damage to the central vein, or else she makes an incision from one side to the very central vein that she damages only superficially. Rarely she would not make any transversal incision, rather taking a partial bite of the leaf stalk.

It is evident from the tables characterizing the leaf rolls (Tabs. VI, VII, and VIII) that in all of the three size categories of damaged leaves incisions starting from the right margin of the blade slightly prevail. On average 51.8% of the leaves of *C. betulus* and 55.7% of the leaves of *C. avellana* were incised from the right side. The cuts into the leaf blades were always near their bases. On the leaves of *C. betulus* and *C. avellana* the central vein was bitten through at an average distance of 7.7 mm and 4.9 mm from the leaf stalk, respectively. With the increasing size of leaves, the incision was slightly shifting towards the apical part. On the leaves of *C. betulus* and *C. avellana*, the mean length of incisions was 13.2 mm and 17.4 mm, respectively. The lengths of transversal incisions in both woody species were growing with the increasing area of the leaves. On the leaves of *C. betulus*, marginal parts of blades connecting the leaf bases with their distal parts were on average 6.2 mm wide, on the leaves of *C. avellana* 8.5 mm wide. The width of this connection was increasing with the increasing leaf area. In the links on the leaves of *C. betulus* of all size categories there were on average 2.1 (on the leaves of *C. avellana* 1.6) lateral veins. In case the transversal sections ended near the lateral vein at the time of blade rolling, their length did not change throughout the period of their occurrence on the trees. In opposite cases, the length of the incisions was moderately increased

VII: *Basic characteristic of A. coryli leaf rolls on C. betulus (in the numerator) and C. avellana (in the denominator) depending on the length of damaged leaves. Presented are total and mean values. The Brno (Vsetín) area 2011, 2012.*

Characteristics	**Length of damaged leaves on C. *betulus*/C. *avellana* (mm)**			
	≤ 60/ ≤ 65	**61–70/ 66–75**	**≥ 71/ ≥ 76**	**Total**
Number of rolls	595/139	539/152	423/122	1 557/413
Length of the damaged leaves (mm)	54.8/59.1	66.5/71.1	78.6/84.2	65.3/70.9
Length of the rolls (mm)	14.6/22.0	16.7/26.0	19.3/29.8	16.6/25.7
Width of the rolls (mm)	6.3/8.3	6.8/9.3	7.4/10.1	6.7/9.2
Length of the transversal sections (mm)	12.1/15.4	13.3/17.7	14.8/19.5	13.2/17.4
Sections from the left (%) (complement to 100% = incisions from the right)	47.5/45.8	48.5/43.7	48.9/43.3	48.2/44.3
Length of the slight tears on blades (mm)	1.8/2.1	2.0/2.6	1.9/2.7	1.9/2.6
Width of the links of blade basal parts with the rolls (mm)	5.5/7.2	6.2/8.3	7.1/9.7	6.2/8.5
Number of lateral leaf veins in the links	2.0/1.6	2.1/1.6	2.1/1.6	2.1/1.6
Distance of bites in central veins from leaf stalks (mm)	6.7/4.3	7.7/5.0	8.9/5.3	7.7/4.9
Number of incisions in central veins	5.6/5.9	6.4/5.9	7.1/6.5	6.3/6.2
Number of incisions in lateral veins	39.2/39.0	44.2/49.4	48.4/41.3	44.1/43.6
Number of eggs in the rolls	1.00/1.24	1.02/1.11	0.93/1.37	0.99/1.22
Order of the rolls from terminal buds	3.4/1.8	3.4/2.0	4.0/2.9	3.5/2.2

VIII: *Basic characteristic of A. coryli leaf rolls on C. betulus (in the numerator) and C. avellana (in the denominator) depending on the width of damaged leaves. Presented are total and mean values. The Brno (Vsetín) area 2011, 2012.*

Characteristics	**Width of damaged leaves on C. *betulus*/C. *avellana* (mm)**			
	≤ 35/ ≤ 50	**36–40/ 51–60**	**≥ 41/ ≥ 61**	**Total**
Number of rolls	723/131	449/145	385/137	1 557/413
Width of the damaged leaves (mm)	32.1/45.7	38.4/56.5	45.3/68.5	37.2/57.0
Length of the rolls (mm)	14.6/21.1	17.1/25.5	19.9/30.6	16.6/25.7
Width of the rolls (mm)	6.3/8.3	6.9/9.1	7.5/10.4	6.7/9.2
Length of the transversal incisions (mm)	12.0/15.0	13.6/17.5	15.1/19.7	13.2/17.4
Incisions from the left (%) (complement to 100% = incisions from the right)	46.3/42.1	48.7/45.1	51.5/44.8	48.2/44.3
Length of the tears on blades (mm)	1.8/2.1	1.8/2.5	2.1/2.7	1.9/2.6
Width of the links of blade basal parts with the rolls (mm)	5.5/6.8	6.4/8.4	7.2/10.5	6.2/8.5
Number of lateral leaf veins in the links	2.0/1.5	2.1/1.6	2.1/1.7	2.1/1.6
Distance of bites in central veins from leaf stalks (mm)	7.0/4.3	8.1/5.0	8.6/5.3	7.7/4.9
Number of incisions in central veins	5.7/5.5	6.4/6.1	7.2/6.4	6.3/6.2
Number of incisions in lateral veins	41.2/41.1	45.2/44.9	47.5/43.9	44.1/43.6
Number of eggs in the rolls	1.01/1.16	0.94/1.19	1.01/1.33	0.99/1.22
Order of the rolls from terminal buds	3.2/1.8	3.6/2.0	4.1/2.7	3.5/2.2

by a slight tearing of the blade at the time of blade rolling and afterwards (in the rolls on *C. betulus* and *C. avellana* on average by 2 mm and 3 mm, respectively) (Tab. IX).

Due to the disruption of the conductive routes, leaf tissues located distally from the incision become gradually withered. Withering of the blade and the consequent suppleness and easier folding are accelerated by deep incisions bitten from the abaxial face of the blade into the central vein and lateral veins. Females bit out 2 to 16 (on average 6.3) incisions into the central vein on the leaves of *C. betulus*. They bit out almost the same number of incisions (two to 12/on average 6.2/) into the central vein on *C. avellana*. The individual incisions were 1 to 10 mm distant from one another, and their size was decreasing towards the apex of the leaf. The females also made numerous series of incisions into the lateral veins on the leaf blade half with the intact margin (i.e. on the half of the blade with the link on which the future roll will be hanging). On average 44 distinct incisions (at the most 110) were bitten out into the lateral veins (Tab. VI, VII, VIII). Moreover, the surfaces of apical

IX: *The average area of the leaves of C. betulus and C. avellana rolled by A. coryli females (incl. of the average length of the slight tear of the blades). Brno area (Vsetín area), 2012.*

Period	*C. betulus*			*C. avellana*		
	Number of rolls	Leaf area rolled (cm²/%)	Length of slight tears on blades (mm)	Number of rolls	Leaf area rolled (cm²/%)	Length of slight tears on blades (mm)
May	53	19.5/90.7	1.5	16	25.3/88.0	0.8
June	176	16.1/90.9	1.7	59	25.3/92.0	2.6
July–August	437	15.1/92.5	1.9	176	26.6/90.1	3.2
Sept.–October	390	13.6/90.0	2.3	71	26.3/86.0	3.3
Total (average)	1056	14.9/91.2	2.0	322	26.2/89.5	3.0

X: *The course of decay of C. betulus and C. avellana leaf blades damaged by the rolls of A. coryli of the 1st generation (in the numerator) and of the 2nd generation (in the denominator). The Brno (Vsetín) area, 2012.*

Month	Rolls on *C. betulus*		Rolls on *C. avellana*	
	Number	Dead leaf area (%)	Number	Dead leaf area (%)
May	53/-	11.4/-	16/-	3.3/-
June	175/-	41.0/-	59/-	33.3/-
July	222/-	69.1/-	46/-	52.6/-
August	189/26	75.3/6.7	121/9	59.0/-
September	204/13	79.2/38.5	35/6	66.0/16.7
October	139/33	88.4/43.0	18/12	71.1/32.9
Total (average)	982/72	67.0/29.0	295/27	51.5/18.3

parts of both main and lateral veins were often bitten almost to the apex or the edge of the blade.

After a certain time, the female returns to the leaf prepared in this way and slightly withered. She folds both halves of the leaf blade along the main vein first with the upper face towards her, the natural tendency of drying out leaves making it easier for her. Then the female starts to roll the folded blade into a short cylindrical roll. She lays her eggs only into the first up to the second fold in the apical part of the blade (at a maximum distance of 10 mm from the tip of the leaf), i.e. into the centre of the prospective roll. The main leaf vein is oriented into the transversal axis of the roll at its upper end, which is ingeniously enclosed by the leaf blade folds. The lower end of the roll is also enclosed by means of the bent leaf margins. An eccentric folding of the leaf along the main vein facilitates closing of the roll. This is because the inner half of the folded leaf (i.e. the half with incisions in lateral veins) is nearly at all times smaller. The female makes use of the overlapping side margin to close the lower end of the roll. Closures on both sides prevent unrolling of the rolls and help to create a suitable environment for the development of *A. coryli* inside of the roll. On the transversal section, the rolls consist of 5 to 10 layers of leaves (depending on the size of the rolled leaf blade). This is why the environment inside the rolls changes only very slowly.

More Detailed Characteristic of the Rolls

The finished rolls are of a roughly cylindrical shape. They hang on the side of the undamaged margin of the blade. Their longitudinal axis is oriented ± on the slant to the leaf stalk and the intact main vein. In the investigated area, an average of 14.9 cm² (89.8%) was rolled, and 1.7 cm² (10.2%) unrolled on the leaves of *C. betulus* of an average area 16.6 cm². On the leaves of *C. avellana* with an average area 29.7 cm², on average 25.6 cm² (86.2%) was rolled and 4.1 cm² (13.8%) unrolled. The rolled leaf area on *C. betulus* was 1.7 times smaller than on *C. avellana*. The size of the rolls depends on the size of the rolled area. The rolls on *C. betulus* were on average 16.6 mm long and 6.7 mm wide. The rolls on *C. avellana* were on average 25.7 mm long and 9.2 mm wide (Tabs. VI, VII, and VIII). The average volume of the rolls on *C. betulus* was 0.6 cm³, on *C. avellana* 1.7 cm³, i.e. 2.8 times larger than on *C. betulus*. There are no data on the size of the rolled area and on the dimensions of the rolls in the available literature.

According to my own observation, the rolls on the trees occur from May till October. The rolled blade, however, starts to wither and die back as early as from the second decade of May. In the course of the vegetation season, the browning up to blackening of the rolls continues. In October 2012, leaf tissues in the rolls of the first generation on *C. betulus* and *C. avellana* were decayed at 88.4% and 71.1%, respectively. On *C. betulus*, the decay of blades in the rolls of the second generation started in August and on *C. avellana* in September. In October, 43.0% of tissues died back in the rolls on *C. betulus* and 32.9% on *C. avellana* (Tab. X). The individual parts of the rolled blade experience an uneven decay. The first to die are tissues in the apical part of the blade that are damaged by feeding of the *A. coryli* larvae. The last to decay are

XI: *The influence of the link width of A. coryli leaf rolls with the unrolled basal part of the leaf blade on the decay of C. betulus and C. avellana leaves. The Brno (Vsetín) area, 2012.*

Rolls on the leaves of *C. betulus*				Rolls on the leaves of *C. avellana*			
Width of the link (mm)	Average width of the link (mm)	% of the green part of the leaf blade		Width of the link (mm)	Average width of the link (mm)	% of the green part of the leaf blade	
		Rolls of the 1st generation	Rolls of the 2nd generation			Rolls of the 1st generation	Rolls of the 2nd generation
≤ 4	3.4	28.4	64.6	≤ 6	4.9	44.0	66.2
5–6	5.6	30.2	70.4	7–10	8.6	46.7	85.8
≥ 7	8.3	38.2	75.1	≥ 11	13.0	57.0	85.6
Average	6.3	33.0	71.0	Average	8.4	48.5	81.7

XII: *The frequency of the occurrence of A. coryli eggs in the rolls and the average area of the rolled leaves on C. betulus (in the numerator) and C. avellana (in the denominator). The Brno (Vsetín) area, 2011, 2012.*

Number of eggs	Number of rolls	(%)	Average leaf area (cm^2)	Number of eggs	(%)
0	180/33	13.1/9.6	18.4/27.6	-	-
1	1 045/226	75.9/65.7	16.2/29.1	1 045/226	76.3/53.7
2	134/63	9.7/18.3	18.1/30.4	268/126	19.6/29.9
3	16/19	1.2/5.5	19.7/32.6	48/57	3.5/13.5
4	2/3	0.1/0.9	15.0/37.0	8/12	0.6/2.9
Total	1 377/344	100.0/100.0	-	1 369/421	100.0/100.0
Average	-	-	16.7/29.5	0.99/1.22	-

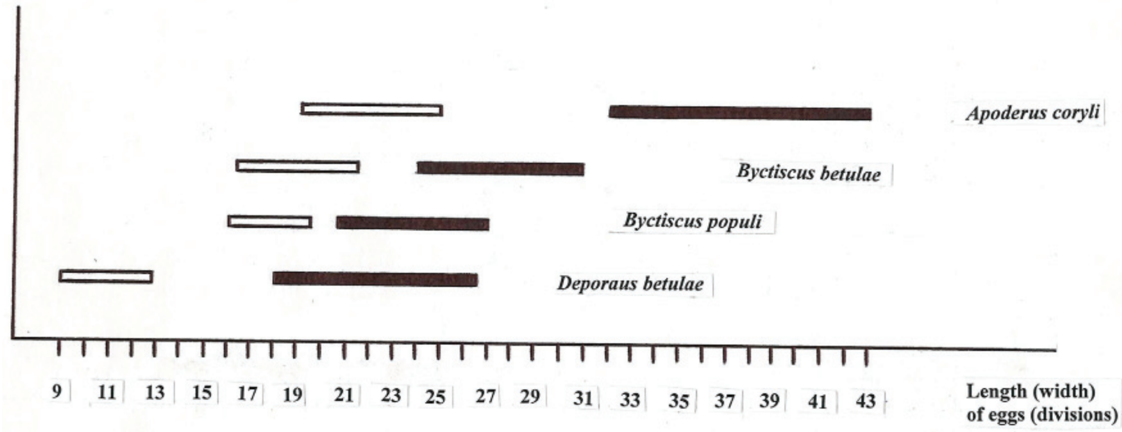
blade parts close to the unbitten lateral veins (i.e. close to the link of the rolls with the unrolled bases of leaves). On both woody species, the dynamics of the decay of tissues in the rolls is influenced by the width of the marginal part of the leaves, by which the rolls are connected with the unrolled leaf bases (Tab. XI).

Rolls of the first generation start to fall from the trees in the second half of July. At the beginning of August 2012, around 5% of rolls fell from *C. betulus*, in September it was around 10% of the rolls. Most of the rolls fell down only during October. Rolls of the second generation fall from the trees as late as towards the end of October, the latest being the beginning of November. Unrolled leaf bases remain green almost throughout the vegetation season, and they mostly remain on the trees until the natural leaf-shedding period. Undamaged leaves on the young and shrubby *C. betulus* usually die earlier than on *C. avellana*. By contrast to *C. avellana*, however, the naturally died leaves remain on *C. betulus* often until the spring of the next year.

Oviposition

In the initial phase of the rolling of blades, the *A. coryli* females lay up usually only one egg (maximum up to four eggs) into the leaf rolls. In the area under study, one egg was found in 75.9% of rolls on *C. betulus* and in 65.7% of rolls on *C. avellana*. No egg was laid up into 13.1% and 9.6% of rolls on *C. betulus* and on *C. avellana*, respectively. On average, the rolls on *C. betulus* contained 1.0 egg and those on *C. avellana* 1.2 eggs (Tab. XII). With the increasing area of the rolled leaves on *C. betulus* the average number of eggs did not change, however the rolls of above-average size on *C. avellana* contained an above-average number (on average 1.45) of eggs (Tab. VI). Sakurai (1986) demonstrated the tendency to multiple ovipositions into larger leaves in the related species of *Apoderus balteatus* Roelofs.

The zone, into which the females lay their eggs, is located in the terminal part of the leaf blade (at a distance within 10 mm from the tip). In the rolls of leaves on *C. betulus* 82.5% of eggs were laid inside of the lap emerged by folding of the blade along the central vein towards its adaxial face. Only 17.5% of eggs were deposited outside of this lap; thus, the eggs came into direct contact with the abaxial face of the blade. In the rolls of leaves on *C. avellana* 67.1% of eggs were laid up inside of the longitudinal lap of the blade with 32.9% of eggs being deposited outside of the lap. Generally, it can be stated that *A. coryli* females lay their eggs mainly inside of the lap after the initial folding of the blade. They mostly place their eggs outside of this lap in multiple ovipositions, both on *C. betulus* and mainly on *C. avellana*. Laying up their eggs into separate places within the roll the females decrease the interference among the larvae living within a relatively confined space. The females of *Apoderus balteatus* Roelofs also deposit their eggs into various places within the roll, thereby instinctively preventing cannibalism on the larvae (Sakurai, 1986).



6: *Dimensions of vital eggs of A. coryli and three species of the Rhynchitidae family (length- dark, width- light) (1 division = 0.0357 mm)*

The eggs of *A. coryli* are yellow to orange, semi-glossy to shiny. Their shape is lengthways oval (rounded cylindrical), with a flexible, firm, and non-sticky chorion. Since the eggs are deposited quite loosely in the rolls, they fall out easily upon unrolling of the rolls. The surface of the eggs is smooth or provided with short pricklets of varying density and 0.03 to 0.04 mm in length either at places or on the full surface area. Freshly laid up eggs are on average 1.27 mm long and 0.81 mm wide. During their embryonic evolution, they become slightly longer and narrower (on average to 1.32 × 0.79 mm). The eggs damaged by endoparasitoids from the family of Trichogrammatidae gradually become brown to black. Their average length increases to 1.39 mm and the width decreases to 0.78 mm. For the dimensions of the vital eggs of *A. coryli* and three abundant species from the family of Rhynchitidae see Fig. 5.

In the females of *A. coryli* the oviposition lasts for almost two months, most often from mid-May till mid-June (Fig. 6). Throughout the reproductive period, the females would produce about 30 rolls and lay up on average 30 eggs. They would damage one leaf (and lay up one egg) approximately in two days.

Embryonic and Postembryonic Evolution

The larvae of the 1st instar emerge from the eggs on average within 10 days (in the laboratory conditions as early as within 5 to 7 days) after oviposition. The head shell of the larvae is 0.60 to 0.78 mm wide. Their bodies are shiny, yellowish, 1.4 to 3.6 (on average 2.5) mm long and 0.7 to 1.2 (on average 0.9) mm wide. They develop on average 7 days (in the laboratory 5 to 6 days). During this time, they damage on average 0.4 cm^2 of leaves. The larvae produce brown to black filamentous frass of the total length of about 1.68 mm, width 0.07 mm, and volume 0.0065 mm^3.

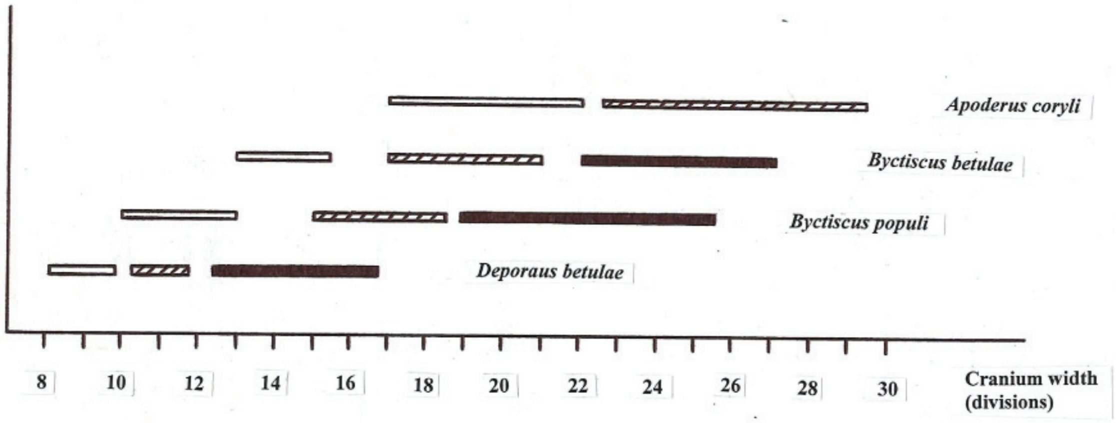
The head shell of the larvae of the 2nd instar is 0.80 to 1.05 mm wide. Their bodies are yellow like yolk to orange, 3 to 8 mm long and 1 to 2.1 mm wide. They develop 2 to 3 weeks (in the laboratory 10 to 12 days). The larvae consume on average 3.6 cm^2 of leaves. They produce brown to black filamentous frass of the entire length 6.77 mm, width 0.15 mm, and volume 0.1196 mm^3. In total, the larvae of both instars damage on average 4 cm^2 of leaves. By contrast to *Deporaus betulae* (L.), *Byctiscus populi* (L.), and *B. betulae* (L.), the development of *A. coryli* larvae consists of only two instars (Fig. 7) (Urban, 2012a, b,c).

Contrary to the representatives of the Rhynchitidae family, the grown-up larvae of *A. coryli* pupate within the rolls, usually on trees (according to some literary data also in the ground). The stage of the pupa lasts on average 7 days (in the laboratory 4 to 6 days). Young beetles of the first generation emerge from mid-June to the end of August. Having rested for several days, the beetles leave the rolls through oval outlet holes of 2 to 4 (on average 3.1) mm in diameter (Fig. 8). The development from the oviposition to the eclosion of beetles takes 5 to 7 weeks, i.e. around one and a half months (around two months according to Escherich, 1923).

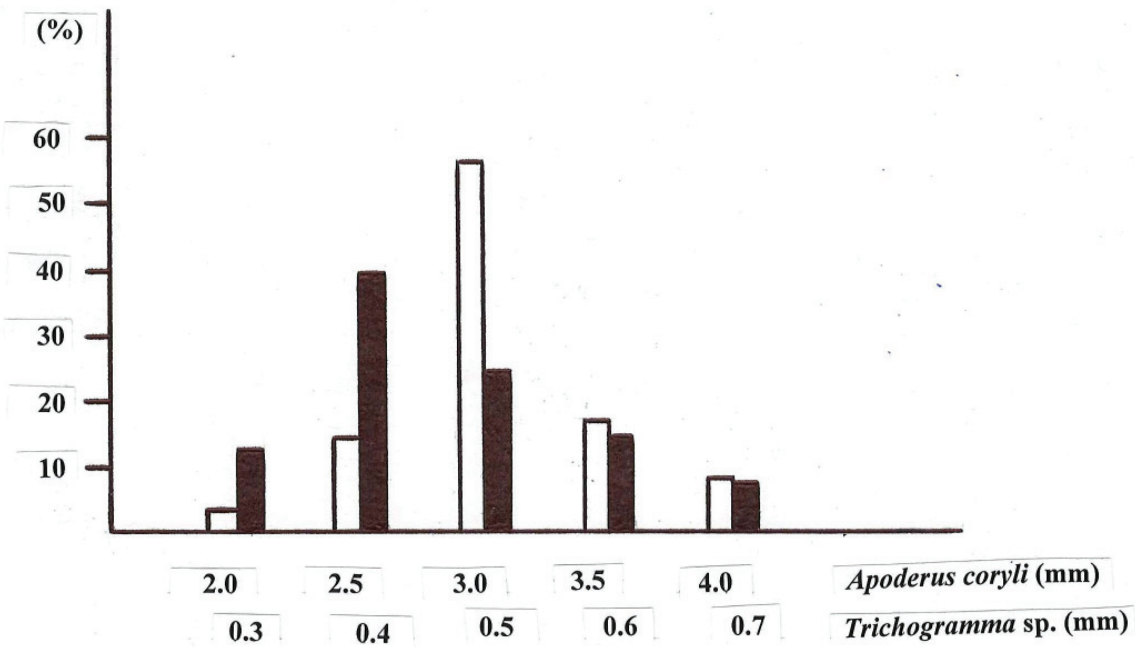
Occurrence of the Beetles of the First and Second Generation

In the Brno region, the beetles of the first generation occurred on the trees from mid-June to the beginning of September. During 3 to 4 weeks in the laboratory, males damaged 11.4 to 16.4 cm^2 (females 18.5 to 30.9 cm^2) of the leaves of *C. avellana* (Tab. XIII). Out of 1 cm^2 of the consumed leaf area, the males produced on average 65 pieces of dark frass sized 1.0 × 0.2 mm. The females produced on average 54 pieces of frass sized 1.1 × 0.3 mm out of 1 cm^2 of the destroyed leaf area.

The beetles that eclosed early (i.e. already in the second half of June) usually mated and founded the second generation, although their fertility was substantially lower as compared with the fertility of the last year's females after wintering (around 11 eggs). However, a vast majority (over ¾) of this year's beetles of the first generation did not



7: *Head widths of the larvae of the individual A. coryli instars and three species of the Rhynchitidae family (1 division = 0.0357 mm). Larvae of the 1st instar are shown in light, larvae of the second instar are dashed, and larvae of the third instar are dark. Larvae of A. coryli develop only through two instars.*



8: *Diameters of flight holes of A. coryli imagoes in the leaf rolls (light columns) and Trichogramma sp. imagoes in the chorions of the A. coryli eggs (dark columns). The Brno (Vsetín) area, 2011, 2012.*

mate, and having finished their maturation feeding, they sought suitable wintering places.

In the open, the rolls made by the females of the first generation were infrequently found from 20 July to 12 October. Larvae developed from the eggs and pupated towards the end of the growing season. The second generation beetles eclosed from 5 September to 25 October, and after a short period of intense feeding they retired into wintering hiding places (Tab. XIII, Fig. 6). According to the literature, the *A. coryli* females establish the second generation under favourable conditions. However, the larvae of this generation allegedly winter, and pupate only in the next spring.

Mortality

The mortality rate of *A. coryli* in the leaf rolls on *C. betulus* and *C. avellana* is high. In the Brno area, the mortality during the growing period was on a quick rise, reaching on average 85% in October and November. The mortality of eggs (on average 55%) was by far the highest. The larvae of the 1st instar exhibited 16% mortality, the larvae of the 2nd instar 11%, and the pupae exhibited a mortality of 3%. Atrophic dead imagoes were found in the rolls sporadically (Tab. XIV). In many localities under study, roe deer browsing destroyed a great part of the rolls on young shoots.

The greatest share in the enormous dying of the eggs had an endoparasitoid tiny wasp

XIII: *The course of leaf damage on C. avellana by this year's imagoes of A. coryli. Imagoes designated by * were reared from the rolls brought to the laboratory (the other imagoes were harvested in the open). Laboratory research, 2011, 2012.*

Date	Damage to the leaves by male imagoes (cm²)					Damage to the leaves by female imagoes (cm²)				
	1st generation 2011	1st generation 2011	1st generation* 2012	1st generation 2012	2nd generation 2012	2nd generation* 2011	1st generation* 2011	1st generation 2011	1st generation 2011	1st generation* 2012
13 July							0			
20 July							6.0			
27 July	0						10.2	0		
3 Aug.	4.7	0					3.8	4.3		
10 Aug.	3.3	5.8					3.8	3.8		
17 Aug.	3.4	5.0					4.7	5.4	0	
24 Aug.	0	1.4	0				2.4	3.8	6.7	0
31 Aug.	0	0	5.9				0	1.9	6.4	5.5
7 Sept.	0	0	5.5	0			0	0	5.7	5.0
14 Sept.	0	0	4.6	4.9	0		0	0	0.1	4.8
21 Sept.	0	0	0.4	5.9	9.8		0	0	+	3.2
28 Sept.	0	0	0	2.4	3.8		+	0		0
5 Oct.	0	+	0	0	0.1			0		0
12 Oct.	0		0	0	0			0		0
19 Oct.	0		0	0	0	0		0		0
26 Oct.	0		+	+	0	3.5		0		0
2 Nov.	0				0	2.7		+		0
9 Nov.	+				+	2.6				0
16 Nov.						0.5				0
23 Nov.						0				0
30 Nov.						0				0
7 Dec.						0				+
Total	11.4	12.2	16.4	13.2	13.7	9.3	30.9	19.2	18.9	18.5

XIV: *The incidence of A. coryli individuals at the respective developmental stages in the rolls on C. betulus and C. avellana. The numerator and the denominator read the living/dead individuals, respectively (%). The Brno (Vsetín) area, 2011, 2012.*

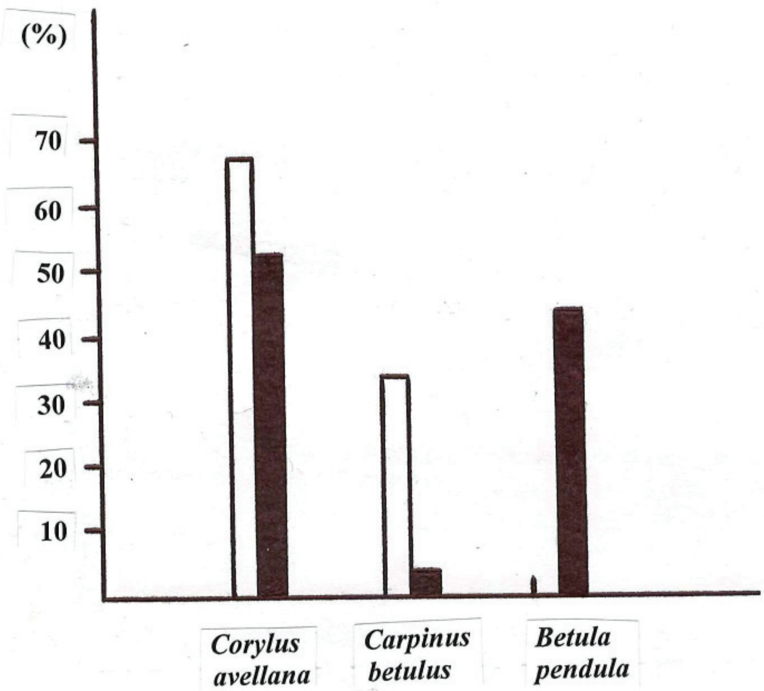
Month	Eggs	Larvae		Pupae	Imagoes		Total living/dead	Total living + dead
		1st instar	2nd instar		in the rolls	abandoned		
May	55.0/22.7	10.0/3.3	6.7/3.3	-	-	-	71.7/28.3	100.0
June	14.2/52.9	4.5/11.0	5.2/4.5	1.9/-	0.7/0.6	4.5	31.0/69.0	100.0
July	11.0/60.8	3.5/12.1	2.0/5.1	-	-	5.5	22.0/78.0	100.0
August	3.8/57.7	1.0/12.7	4.6/7.9	0.5/0.3	-/0.5	11.0	20.9/79.1	100.0
September	3.5/54.5	0.2/15.7	1.2/10.5	-/0.2	0.2/0.4	13.6	18.7/81.3	100.0
October	3.9/52.6	0.3/16.3	0.6/11.5	0.3/1.8	-	12.7	17.8/82.2	100.0
November	-/57.7	-/15.4	-/11.5	-/3.9	-	11.5	11.5/88.5	100.0
Average	7.3/54.6	1.6/13.8	2.5/8.6	0.3/0.5	0.1/0.3	10.4	22.2/77.8	100.0

of the Trichogrammatidae family. In 2012, the first eggs infested by this wasp were found as early as towards the end of May. The percentage of the infested eggs culminated in July, in which month the wasp killed almost 43% of the *A. coryli* subpopulation within the rolls (Tab. XV). In case there were more *A. coryli* eggs occurring in the rolls, the wasps usually placed their eggs into all. Brown to black colouring of the eggs infested by the parasite makes them easily discernible from vital eggs. As against healthy eggs, the infested eggs are on average somewhat longer and narrower.

The first eggs of *A. coryli* that were left by the flown out imagoes of the parasitoid were found as early as on 13 June. The complete development of the wasp took only two weeks. The wasps leave

XV: *Impact of mortality factors on the development of A. coryli in the rolls of C. betulus and C. avellana leaves. The Brno (Vsetín) area, 2012.*

Month	Undisturbed development (count/%)	Disturbed development (count/%)						Total
		Tricho-gramma sp.	Cecidomyi-idae g. sp.	Lepidoptera (*Anacampsis populella* etc.)	Insect ectoparasi-toids	Unknown factors	Total	
May	43/71.7	2/3.3	14/23.3	1/1.7	-	-	17/28.3	60/100.0
June	48/31.0	30/19.3	38/24.5	9/5.8	8/5.2	22/14.2	107/69.0	155/100.0
July	39/17.6	94/42.5	38/17.2	5/2.3	2/0.9	43/19.5	182/82.4	221/100.0
August	66/22.1	110/36.8	48/16.0	6/2.0	15/5.0	54/18.1	233/77.9	299/100.0
Sept.	42/17.6	104/43.7	48/20.2	10/4.2	1/0.4	33/13.9	196/82.4	238/100.0
Oct.	29/15.0	74/38.3	47/24.4	5/2.6	1/0.5	37/19.2	164/85.0	193/100.0
Total	267/22.9	414/35.5	233/20.0	36/3.1	27/2.3	189/16.2	899/77.1	1 166/100.0



9: *Food preferences of the last year's imagoes (light) and this year's (freshly eclosed) imagoes of A. coryli (dark). Laboratory research, 2011, 2012.*

the eggs through oval flight holes 0.3 to 0.7 mm in diameter, which are always located at the end of the eggs. The females of the parasitoid bite their way into the rolls through all layers creating a small corridor 0.5 to 0.8 mm in diameter. Young wasps leave the rolls either through this alien aperture or a hole of their own. The mortality rate of the parasitoid in the eggs of *A. coryli* is high (on average 80%). Eggs and larvae of the wasp die most frequently, pupae and imagoes less often. Dead adult wasps were found both in the egg membranes of *A. coryli* and inside of the rolls. There are no references to endoparasitoids of eggs from the family Trichogrammatidae in the available literature. *Trichogramma dendrolimi* Matsum develops in the eggs of the related species *Deporaus betulae* (L.) (Polaszek, 2010). *Ophioneurus signatus* Ratz. (Trichogrammatidae) was reared from the eggs of *Byctiscus betulae* (L.) and *Involvulus caeruleus* (Deg.) (Nikolskaja & Trjapicyn, 1978).

Eggs and larvae of *A. coryli* are very often infested by saproparasitic larvae of the Cecidomyiidae family. The larvae are whitish, light red to orange and up to 2 mm in length. In 2012, gall midges killed on average 20% of the subpopulation of *A. coryli* in the rolls (Tab. XV). The saprotrophic ability of gall midges is evidenced by the fact that the larvae of *A. coryli* accomplish their development only in a small proportion of leaf rolls occupied by gall midges. On average one gall midge developed in 53.4% of the rolls, two gall midges developed in 28.4% of the rolls, three developed in 12.5% of the rolls, and four to ten gall midges developed in 5.7% of the rolls. The first larvae 0.8 to 1.2 mm in length were found in mid-May and the first abandoned puparia were found at the beginning of July. We can assume that the females of gall midges lay their eggs at the time of leaf rolling, and that the development of gall midges is univoltine.

Eggs, caterpillars, and pupae of the polyphagous species *Anacampsis populella* (Cl.) (Gelechiidae) and of some representatives of the Tortricidae family are quite often found developing in the rolls of *A. coryli*. In surroundings of Brno (Vsetín) city on average 3.1% of the rolls were damaged by the Lepidoptera caterpillars. A solitary representative of the Braconidae family rarely had its share in the mortality. Its larvae developed as ectoparasitoids on the larvae of the 2nd instar. From mid-June and in July the larvae made oval, yellowish-brown cocoons 2 to 4 mm in length and 1.1 to 1.4 mm in width. The larvae of Neuroptera, the larvae and nymphs of Thysanoptera, the larvae from the family of Syrphidae, the larvae, nymphs and imagoes from the family of Trombididae, and nymphs and imagoes of *Anthocoris nemorum* L. were rarely found within the rolls. Towards the end of the growing period, imagoes of *Coccinella septempunctata* L. were often found hiding in old rolls or in rolls damaged by caterpillars. On average 16.2% of *A. coryli* died in the rolls due to unknown endogenous and exogenous causes (Tab. XV).

Harmfulness

Apoderus coryli is a widely spread and abundant representative of the Attelabidae family. In the Brno area it develops mainly on *C. betulus* and often also on *C. avellana*, although in the laboratory the last year's imagoes caused damage to *C. avellana* twice as much as to *C. betulus*. By contrast, current year's imagoes caused very little harm to *C. betulus* (Fig. 9). The beetles damage the leaves of young (mostly 5 to 15 year old) trees, making windows and rolls. During the 1.5 to 2 month period of reproduction, the males and females (after wintering) consumed on average 21 and 33 cm^2 of leaves, respectively. The damaged area corresponded to 1.2 (or 1.9) leaves of *C. betulus* (of an average area of 17 cm^2), and 0.7 (or 1.1) leaves of *C. avellana* (of an average area of 30 cm^2). In the course of 3 to 4 weeks, the males and females of the first (second) generation consumed on average 15 and 25 cm^2 of leaves, respectively. The damaged area corresponded to 0.9 (or 1.5) leaves of *C. betulus* (of an average area of 17 cm^2) and 0.5 (or 0.8) leaves of *C. avellana* (of an average area of 30 cm^2). The female after wintering made on average 30 rolls, and those of the first generation made on average 11 rolls. After the wintering period, females caused damage by leaf rolling of an area on average 8.3 times larger on *C. betulus* (13.9 times on *C. avellana*) than beetles during the maturation feeding. Females of the first generation damaged by leaf rolling on average by 4.1 times larger area on *C. betulus* (6.9 times on *C. avellana*) than beetles during the maturation feeding. It follows that the rolled leaf area is 4.1 to 13.9 times (on average 9 times) larger than the area destroyed by the consumption of leaves. The assimilation function of the leaf tissues within the rolls is minimal and of short-term character. Therefore, the rolling of leaves means a much greater physiological damage to trees than the maturation feeding of the beetles.

Localization of the rolls and the area of undamaged neighbouring leaf below and above the roll on the shoots of *C. betulus* and *C. avellana* were recorded from June to October 2012. On the shoots of *C. betulus*, the rolls occurred on the 1st to the 15th (on average 3.7) leaf from the apex. Rolls on fast-growing sprouts were the lowest (on the 10th to the 15th leaf). The order of the leaves with the rolls continuously increased (from 2.3 to 4.4) from June till October. The average area of the rolled leaves of *C. betulus* (16.0 cm^2) was basically equal to the area of undamaged leaves below the rolls (17.2 cm^2) and above the rolls (16.3 cm^2). On the shoots of *C. avellana*, the rolls occurred on the 1st to the 10th (on average 2.1) leaf from the apex. The order of leaves with rolls slightly increased from June to October (from 1.5 to 2.3). The average area of rolled leaves (30.0 cm^2) was by 50 (or 41) per cent lower than the area of undamaged leaves below the rolls (45.0 cm^2) and above the rolls (42.4 cm^2). It ensued from the investigation that on *C. betulus* the females of *A. coryli* mostly rolled the grown up leaves, whereas on *C. avellana*, they usually rolled the growing up leaves. It is probable that the loss in the leaf area of *C. avellana* is partly compensated by the increased area of intact neighbouring leaves.

Opinions about the harmfulness of *A. coryli* rather vary. According to Francke-Grosmann (1974), the species' significance in forestry is negligible. On the other hand, e.g. Escherich (1923) considers *A. coryli* an important pest in forestry since it often causes a significant damage to leaves. Pavlenko & Gorbunov (1985) claim that *A. coryli* causes damage to *C. avellana* and *C. maxima* Mill. in the protective steppic shelterbelts (and mainly forest steppe) zones of Ukraine. Gantner (2001) and Gantner & Jaskiewicz (2002) consider the species as a pest in the plantations of large-fruited *C. avellana* in SE Poland.

A. coryli is responsible for a considerable damage in the production plantations of hazel, where it can be controlled mainly by chemical methods. According to the older entomological and plant protection literature, the pest can be eliminated by collecting (or shaking down) the conspicuous beetles or by collecting the characteristic rolls (Burket, 1927; Baudyš, 1951 a. o.).

SUMMARY

We studied the incidence, evolution and harmfulness of *Apoderus coryli* (L.) (Attelabidae) in the Brno area in 2011 and 2012. The major findings are as follows:

1. Imagoes that occur on trees from the beginning of May to the end of July winter in the studied area. They bite out oval feeding notches sized ca. 8.6 mm^2 in the leaves. The feeding notches on the leaves of *Carpinus betulus* are smaller than those on the leaves of *Corylus avellana*. The average area of the feeding notches decreases with the age of the leaves. Males consume on average 21 (females 33) cm^2 of leaves. They feed mainly during the night, at which time they make around 70% of the feeding notches.
2. After 1 to 3 days of the maturation feeding, the beetles mate for the first time. In the open, the copulating couples can be encountered most often in May. In confinement, the beetles mated on average 3.3 times a day for the period of 50 minutes. Most often (2.8 times), they copulated during the light part of the day (from 6 a.m. to 6 p.m.).
3. The females make a single-sided transversal section nearby the basal part of the leaf blade. On the leaves of *C. betulus*, the section ends on average 6.2 (on *C. avellana* 8.5) mm from the opposite margin of the blade. On *C betulus*, the central vein is intersected at an average distance of 7.7 (on *C. avellana* 4.9) mm from the leaf stalk. The unbitten marginal part of the leaf blade on *C. betulus* is reinforced by on average 2.1 (on *C. avellana* 1.6) lateral veins. The female bites out on average 6.3 conspicuous incisions into the central vein, making on average 44 incisions into the lateral veins (located on the half of the blade with undamaged leaf margin).
4. The female folds the slightly withered part of the blade along its central vein with the adaxial face towards herself. Then female rolls the folded blade starting from the apex of the leaf into a cylindrical roll that is subsequently closed on both sides. On the leaves of *C. betulus* of the average area 16.6 cm^2, female would roll on average 14.9 cm^2 (89.8%). On the leaves of *C. avellana* of the average area 29.7 cm^2, female would roll on average 25.6 cm^2 (86.2%). The rolls on *C. betulus* are on average 16.6 mm long and 6.7 mm wide; the rolls on *C. avellana* are on average 25.7 mm long and 9.2 mm wide.
5. In the initial stage of leaf rolling, the females lay eggs loosely into the folds of the leaf (at a distance of up to 10 mm from the leaf apex). They lay up on average 1.0 and 1.2 eggs into the rolls on *C. betulus* and on *C. avellana*, respectively. The eggs are of oval cylindrical shape, on average 1.27 mm long and 0.81 mm wide. Throughout the period of reproduction, the female make around 30 rolls and lay up about 30 eggs.
6. Larvae of the 1st instar emerge from the eggs in 10 days. During a week of feeding, the larvae damage about 0.4 cm^2 of leaf area. Larvae of the 2nd instar develop for 2 to 3 weeks and damage about 3.6 cm^2 of leaves. Grown-up larvae of the 2nd instar pupate within the rolls. The development from the oviposition to the emergence of beetles from the rolls takes 5 to 7 weeks.
7. Beetles of the 1st generation were found on the trees from mid-June to the beginning of September. In the laboratory, males damaged on average the leaf area of 13.9 (females 24.7) cm^2 during 3–4 weeks. Most of the beetles of this generation left for their wintering places. Only the early-emerged beetles established the second generation. As compared with the last year's females, their fertility was markedly lower (on average 11 eggs). Beetles of the 2nd generation hatched from the beginning of September to mid-October and sought wintering grounds after a brief period of feeding.
8. Around 85% of individuals died within the rolls (55% of eggs, 16% of larvae of the 1st instar, 11% of larvae of the 2nd instar, 3% of pupae, and sporadically also the freshly emerged imagoes). The greatest share in the mortality of eggs had the polyvoltine endoparasitoid wasp from the family of Trichogrammatidae. Eggs and larvae of *A. coryli* were very often infested by saproparasitic larvae from the Cecidomyiidae family.
9. In the Brno area, *A. coryli* develops mainly on *C. betulus* and often on *C. avellana*, rather scarcely on *Alnus glutinosa*. After their wintering, the females caused damage by leaf rolling on *C. betulus* on a 8.3 times (on *C. avellana* 13.9 times) larger area than the beetles during their maturation feeding. The females of the 1st generation caused damage on *C. betulus* on a 4.1 times (on *C. avellana* 6.9 times) larger area than the beetles during their maturation feeding. Leaf rolling causes a much greater damage to the trees than the maturation feeding of the beetles. On the shoots of *C. betulus*, rolls occurred on average in 3.7 leaves from the apex, on *C. avellana* on average in 2.1 leaves from the apex. On *C. betulus*, the females mostly rolled the full-grown leaves, whereas on *C. avellana*, they mostly rolled the growing leaves.

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