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ATTELABUS NITENS (SCOP.) – AN ABUNDANT BUT BIOLOGICALLY LITTLE KNOWN SPECIES FROM THE FAMILY OF ATTELABIDAE (COLEOPTERA)

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Abstract

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The study deals with the biology of *Attelabus nitens* (Scop.) in the Brno region. In the growing season of 2014, 35 field inspections were made at 10 sites in the intervals of three-to-seven days. Leaf rolls were found on *Quercus petraea*, *Q. dalechampii*, *Q. robur*, *Q. pubescens* and *Q. cerris*, rarely on *Castanea sativa*. Hibernating in the shed leaf rolls are larvae of the second instar. These pupate in the rolls during the second half of April and beginning of May. At the turn of April and May, beetles fly onto host woody plants of the 1st age class. They damage about 30 cm^2 of leaves in two months. Females create about 30 leaf rolls into which they lay 1 to 5 (on average 1.1) eggs. The species develops through two larval instars, which damage 1.7 to 2.3 cm^2 of leaves and come of age towards the end of the growing season. On the primary shoots of oaks (with relatively large leaves), the females rolled below-average sized leaves. On the secondary shoots (with relatively small leaves), they rolled leaves of average to above-average size. The female gnaws a deep mine into the main vein (in a third of its length) from the adaxial side first. Then she makes a cross cut into the blade from both sides up to the main vein, which is damaged only on the surface. Into thicker sections of veins she bites out (mainly from the abaxial side) on average 350 cross cuts. Only then, the female folds the wilted leaf part adaxially along the main vein and after having laid an egg (eggs), she rolls the blade from the end into a transversal cylindrical roll. On the leaves of *Quercus* spp. with an average area of 14.3 cm^2, the females roll on average 11.9 cm^2 (83.2 %). During the growing period, 36 % of individuals died in the leaf rolls on primary shoots and 28 % of individuals died in the leaf rolls on secondary shoots.

Keywords: *Attelabus nitens*, Attelabidae, host woody plants, occurrence, creation of leaf rolls, development, mortality factors, economic importance

INTRODUCTION

Oak leaf roller (*Attelabus nitens* /Scop./) (syn. *A. curculionoides* L. = *Curculio nitens* Scop.) is an abundant and widespread representative of the Attelabidae family. Together with morphologically and biologically related species from the family of Rhynchitidae, species of this family are collectively referred to as leaf-rolling weevils. The systematic position of this immensely interesting and rich-in-species group of leaf-rolling weevils within beetles from the Curculionoidea superfamily is not yet settled. Out of about 1,100 taxa of the Rhynchitidae family and about 1,000 taxa from the Attelabidae family, a larger part occurs in subtropical and tropical zones. In the western part of the Palaearctic region, the family of Rhynchitidae is represented by only 60–70 species and the family of Attelabidae by mere 8 species (Legalov, 2003). In the entomofauna of the Czech Republic, the Rhynchitidae family is represented by 29 species and the Attelabidae family by 3 species (Strejček, 1993). These include several pests in agriculture, fruit and vine growing. Their significance in forestry is as a rule low and they do harm to young trees only locally.

Species of leaf-rolling weevils from the Rhynchitidae family notable in forestry are *Deporaus betulae* (L.), *Byctiscus betulae* (L.) and *B. populi* (L.), from the Attelabidae family then *Apoderus coryli* (L.) and *Attelabus nitens* (Scop.). Incidence, development and harmfulness of the first four above-mentioned species were studied by Urban (2012 a, b, c, 2014 and 2015). This article brings results of studying *A. nitens*, which is a common and natural component of oak stands entomofauna in the Czech Republic. Beetles of this species are very conspicuous and easy to identify. Females create species-specific leaf rolls that demonstrate a strong instinct of the maternal care of the offspring. Prior to rolling, they cut the leaves transversally on both sides up to the main vein. Then they fold the distal blade part along the main vein and roll it into a neat cylinder-shaped roll from the leaf end. There are surprisingly only few detailed works on the biology of *A. nitens* and special studies about the species are almost non-existent.

Geographical Distribution

Attelabus nitens is a West Palaearctic species with the centre of distribution in Europe. Legalov and Friedman (2007) mention its occurrence in 24 European countries and in 7 countries of Asia Minor, Asia Anterior and Central Asia (Georgia, Armenia, Azerbaijan, Turkmenistan, Asian part of Turkey, Syria and Israel). According to some authors (Formánek, 1911; Schaufuss, 1916; Lohse, 1981; Podlussány, 1984), its natural range includes Siberia, too. Opanasenko and Legalov (1996) and Legalov (2002, 2010) inform however that it has not yet been found in the Asian part of Russia where it is substituted by *A. cyanellus* Voss. In the east of Russia, the species reaches as far as into the eastern region of Baskortostan (Legalov, 2007; Legalov *et al.*, 2007). The southern boundary of the natural range cuts the northern mountainous part of Israel (Legalov and Friedman, 2007). It is mentioned to occur in Syria (Weil *et al.*, 2011), southern Turkey (Avgın and Colonnelli, 2011), Greece (Bohr, Winkelmann and Bayer, 2011; Kalapanida and Petrakis, 2012), almost in entire Italy incl. Sicily and Sardinia (Andreetti and Osella, 1994; Abbazzi *et al.*, 1995; Campobasso *et al.*, 1999; Stejskal, 2004) and northern Algeria (Benia and Bounechada, 2011). The western boundary of the natural range runs through the Iberian Peninsula (Alonso-Zarazaga, 2002; Sáez Bolaño *et al.*, 2013), France (Marre, 1916; Legalov and Friedman, 2007), and British Islands (Ritchie, 1916; May, 1993). In the North, it reaches into southern Scandinavia (Francke-Grosmann, 1974) and into the Baltic countries – Lithuania and Latvia (Telnov, 2004; Alekseev, 2005; Tamutis, Tamute and Ferenca, 2011).

In the Czech Republic, *A. nitens* is a common leaf-roller weevil species. It occurs in all localities with its host trees (*Quercus* spp.), i.e. namely in lowlands and warm uplands.

Host Woody Species

Attelabus nitens is a polyphagous species with pronounced tendencies to oligophagy. Its main hosts are various oak species (*Quercus* spp.) (family of Fagaceae). By this tree species the weevil is known in most national languages (e.g. "*zobonoska dubová*", formerly "*tlustonosec dubový*" in Czech, "*nosánik dubový*" in Slovak, "*Eichenblattroller, Eichenroller, Roter Eichenkugelrüssler, Eichen Afterrüsselkäfer, Eichenwickler* a.o." in German, "*trubkovërt dubovyj*" in Russian, "*podryj dębowiec*" in Polish, "*eikenbladroller*" in Dutch, "*Attelabo della quercia*" in Italian etc.).

Some literary sources identify trophic links of the oak leaf roller to specific species of genus *Quercus*. In central Europe, Scherf (1964) observed it on *Q. robur* L., *Q. petraea* (Matt.) Liebl. and *Q. ilex* L. According to Gusev and Rimskij-Korsakov (1953), the species occurs in the European part of the former USSR on *Q. robur*, *Q. petraea* and *Q. pubescens* Willd. In northeast Poland, it damages mainly *Q. robur* (Sprick and Floren, 2007), in northern Italy *Q. cerris* L. and *Q. pubescens* (Maresi and Salvadori, 2004), in Montenegro *Q. pubescens* (Roganović, 2012), in northeast Algeria *Q. ilex* (Benia and Bounechada, 2011), in Spain *Q. faginea* Lam. (Ribes, 2011) and in Israel *Q. boissieri* Reut. (Friedman, 2009).

Regarding the thermophily of most *Quercus* genus species, the spectrum of oak species in southern Europe is more abundant than in central Europe. Oak species reaching into northern Europe (up to southern parts of Scandinavia) are only *Q. robur* and *Q. petraea*. The most widespread European oak species is *Q. robur*, which is missing only in the southern part of the Iberian peninsula, on some islands in the Mediterranean Sea, in Greece and Turkey. Another very widely spread oak species in western, central and southeast Europe is *Q. petraea*. Both these oak species are the most frequent potential hosts of *A. nitens* in Europe.

Apart from *Quercus* spp., the weevil *A. nitens* often infests *Castanea sativa* Mill. (Klapálek, 1903; Marre, 1916; Nüsslin and Rhumbler, 1922; Escherich, 1923; Daanje, 1957; Schwerdtfeger, 1970; Dieckmann, 1974; Podlussány, 1984; Meier *et al.*, 2008; Juhásová *et al.*, 2010; Avgın and Colonnelli, 2011; Guéorguiev, 2011). The abundant occurrence on *C. sativa* is reflected in its alternative (local) German name – Kastanienblattroller. According to Siegel (1866), Francke-Grosmann (1974) and Lohse (1981), the species can develop on *Quercus*, *Alnus* and *Corylus*, according to Formánek (1911), Reitter (1916), Schaufuss (1916), Roubal (1937–1941) and Pfeifer (1964) on *Quercus*, *Corylus* and *Salix*. Legalov, Ghahari and Arzanov (2010) consider its hosts to be *Quercus*, *Alnus* and *Acer*. The widest range of hosts mentions Hoffmann (1958), according to whom the leaf roller weevil lives on *Quercus*, *Castanea*, *Corylus*, *Salix*, *Fagus*, *Carpinus* and *Betula*.

Biology and Economic Significance

Females of *A. nitens* create rolls from the middle and apical part of leaf blade. According to published information, they bite through the blade by two cross cuts, which run from the left and right leaf edge and end at one point on the main leaf vein. Then they usually mildly gnaw the main vein at the contact point of the two cuts, and create a number of incisions into the main vein (as well as into lateral veins) in the rolled part of the blade, which make the subsequent rolling easier. According to sporadic literary data, the females enhance blade pliability also by abundant injuries caused by curved spines on the tibiae of their front legs. The incised part of the leaf remains connected with the basal part of the leaf only by the main vein. After a certain time, the females return to rapidly wilting leaf parts and fold both leaf halves along the main vein with the adaxial side inwards. Subsequently, they lay one or more eggs into the leaf fold and roll the blade from the apical part into a cylinder-shaped roll. The roll is transversal, connected with the green leaf base by means of the main vein, which stiffens the upper margin of the roll. Larvae emerging from the eggs feed on wilted and later slightly disintegrated internal tissues of the leaf roll. Grown-up larvae hibernate in the rolls and pupate in them in the spring. According to some unsubstantiated data, the larvae leave the rolls in the spring and pupate in the ground.

Basic data on *A. nitens* biology are presented in numerous entomological and entomologico-environmental studies (Lampert, 1909; Schaufuss, 1916; Nüsslin and Rhumbler, 1922; Escherich, 1923; Voss, 1932; Živojinovič, 1948; Brauns, 1964; Scherf, 1964; Smith, 1970; Francke-Grosmann, 1974; Nienhaus, Butin and Böhmer, 1992; Stejskal and Trnka, 2013). Ševyrev (1914), Prell (1925) and Daanje (1957) describe the rolling of leaves. Silvestri (1916), Clausen (1940), Nikolskaja (1952), Scherf (1964), Subba Rao (1969), Nikolskaja and Trjapicyn (1978), Kopelke (1983), Knutelski (2007), Ribes (2011) and other authors inform of insect parasitoids in eggs and larvae. Interesting findings brings the histological examination of brain in three leaf-rolling weevil species (*A. nitens*, *Apoderus coryli* /L./ and *Deporaus betulae* /L./) and one species living in leaf rolls created by *A. nitens* (i.e. *Lasiorhynchites sericeus* /Hbst./) (Rossbach, 1962). Regarding the low importance of the species in forestry, there is only very few data about protective and defensive measures against *A. nitens* (Goloverda and Mozoľ, 1977; Mingaleva, Pestov and Zagirova, 2011).

MATERIALS AND METHODS

Oak leaf roller (*A. nitens*) was systematically studied in 2014 at ten sites in the Brno region. Thirty-five field inspections were made during the growing period at intervals of three to seven days. Forest stands situated north of Brno at the Training Forest Enterprise Masaryk Forest Křtiny (TFE Křtiny) were visited twenty times (forest districts of Vranov and Bílovice n. Svitavou). Twelve inspections were made in forests managed by the Forest Administration Brno (Forests of the City of Brno /Lesy města Brna, a.s./ with headquarters in Kuřim) (localities of Kamenný vrch, Komín, Žabovřesky, Červený kopec and Podkomorské lesy). Twice visited were forest stands in the Pozořice forest district (Horákov locality) belonging to the Forest Administration Bučovice (Lesy ČR, s.p. /Forests of the Czech Republic, State Enterprise/) and one field trip was made to Belcredi private forests (nature preserve of Velký Hornek in the southern part of the Moravian Karst Protected Landscape Area). The studied sites were situated up to max. ten kilometres from the city of Brno.

The research was conducted mainly in oak stands of the 1st age class and was focused also on the lower parts of the crowns of older oak trees including self-seeded young trees in the undergrowth or solitary standing. Field observations, the collection of beetles and the sampling of shoots with leaf rolls took place at the time between 09.00 and 15.00 o'clock. In the laboratory, adults were placed into glass dishes with the diameter of 20 cm and height of 8 cm. For breeding, we used freshly cut leafy sections of tree shoots. Bases of the shoots were inserted into small receptacles with water and necks of the receptacles were sealed with paper wadding. The imagos were offered fresh shoots at week intervals, and parameters recorded were longevity, size of damaged leaf area (mm^2), defecation, number of laid eggs, number of eggs in the ovaries of dead females etc.

Annual shoots with leaf rolls were subjected to a detailed examination in the laboratory. We assessed altogether 217 primary (spring) shoots and 119 shoots with the primary and secondary (so-called Lammas) increment. The annual primary shoots without the secondary increment were evaluated separately from the annual shoots with both primary and secondary increment. Recorded parameters included among others the length of shoots (cm), total number of leaves (of these the number of leaf rolls), area of damaged leaves and area of intact leaves (cm^2). Parameters ascertained in damaged leaves included the length and width of leaf rolls (mm), length and width of basal (i.e. unrolled) leaf parts and rolled leaf parts (mm) and their area (cm^2). The number of eggs and larvae, their size and health condition was examined microscopically. Growth stage (instar) of the larvae was determined according to micrometrically measured head case (cranium) width. Larvae of individual instars were monitored for the size of damaged leaf area, defecation, health condition etc.

In 2014, we collected 1,165 leaf rolls of *A. nitens* in the open and placed them in the glass dishes (with a 5 cm layer of garden soil). In winter, the dishes were kept outdoors. In the spring of 2015, we determined the wintering place and pupation of the larvae and the length of pupal stage. A portion of the leaf rolls was placed into photoeclectors in the laboratory conditions to monitor among other things the course of eclosion of *A. nitens* imagos and their parasitoids.

RESULTS AND DISCUSSION

Host Woody Plants

According to literature, *A. nitens* occurs on woody plants of nine different genera. Most often it is reported on *Quercus* spp. and very often also on *Castanea sativa* Mill. Tree species considered as hosts sometimes too are *Alnus* and *Corylus*, rarely *Salix*, sporadically *Fagus*, *Carpinus*, *Betula* and *Acer*. All these tree species (with the exception of *Castanea*) were richly represented in the Brno region. Nevertheless, leaf rolls were found only on the *Quercus* spp. and sporadically on *C. sativa*. Host species were *Q. petraea* (Matt.) Liebl. (65.9 %), *Q. dalechampii* Ten. (22.0 %), *Q. robur* L. (7.3 %), *Q. pubescens* Willd. (2.4 %) and *Q. cerris* L. (2.4 %). The oak leaf roller was never observed on other woody plants in the Brno region, even during the previous years of studying *Byctiscus populi* (L.), *B. betulae* (L.), *Deporaus betulae* (L.) and *Apoderus coryli* (L.). Therefore, it can be stated with a high probability that *A. nitens* occurs in central Moravia only on autochthonous (possibly also on introduced) *Quercus* spp. and on the locally planted allochthonous *C. sativa*. Data about the occurrence on *Alnus* and *Corylus* are mostly older and their objectivity is questionable. *Fagus*, *Carpinus*, *Betula*, *Acer* and apparently *Salix* too should be excluded from the featured host trees.

The oak leaf roller infests preferably young trees of the 1st age class, i.e. grown-up transplants, advance regeneration and young growths (up to height of 3 m), frequently causing damage also to leaves on young coppice shoots. The leaf rolls rarely occur on the lower branches of older trees (up to height of 5 m). It normally damages young shrubby oaks in open older stands, young oak trees on clear cuts, along roads, cleared forest boundary lines, forest stand margins, in parks, botanical gardens etc.

Wintering Stage

The larvae of *A. nitens* develop in leaf rolls and come of age in the period from the end of summer to the beginning of autumn. The grown-up larvae create spacious small cavities inside the rolls, which are lined with the tiny residues of plant tissues and frass pellets hardened by the secretion of accessory glands. A greater part of the larvae (over 80 %) hibernates in leaf rolls fallen onto the ground, and only a small part of them (below 20 %) winter in leaf rolls on the trees. In the spring (usually in the second half of April), the larvae pupate in the rolls. Pupa is 3–6 mm long, yellow, mobile only to a limited extent. Beetles emerge after a period of pupal stage, which lasts from 10 to 17 days. After one or two days of the resting period, the beetles leave the sites of their development and appear in the open.

As to the hibernation of *A. nitens* at the stage of grown-up larvae, the literary opinions agree. Opinions about the place of their pupation differ though. According to the hitherto prevailing opinion, the larvae leave the leaf rolls after hibernation and crawl into the ground. There, they create roomy pupal chambers with smoothed walls in which they pupate (Escherich, 1923; Živojinović, 1948; Brauns, 1964; Koehler and Schnaider, 1972; Francke-Grosmann, 1974; Lohse, 1981; Amann, 1995; Anonymus, 2013). According to Lampert (1909), the larvae leave the rolls as early as in the autumn and crawl into the ground for the pupation. According to Scherf (1964), the larvae pupate within the leaf rolls after hibernation towards the end of April and beginning of May.

Occurrence of Beetles on Trees and their Maturation Feeding

The larvae of *A. nitens* pupate at all times only after hibernation. This is why their development takes a much longer time than that of e.g. the larvae of *Apoderus coryli* or *Byctiscus betulae*, in which young beetles are hibernating (in *A. coryli* rarely also second-generation beetles). The beetles begin to appear on the host species from the end of April (exceptionally as early as from mid-April) and beginning of May.

Beetles from last year's rolls transferred from the outdoor environment into the laboratory on 1th April 2015 were emerging from 7th to 21th April. The total number of emerged beetles amounted to 555 (251 males and 304 females). The sex ratio was 0.8:1 (sexual index 0.55). Individuals of both sexes were emerging concurrently; however, the numbers of males and females exhibited protandry. The numbers of males and females emerged in the 1st, 2nd, 3rd and 4th quarter of the breeding season amounted to 61 (30) – sex ratio 2.0 : 1.0, 135 (170) – sex ratio 0.8 : 1.0, 43 (86) – sex ratio 0.5 : 1.0, and 12 (18) – sex ratio 0.7 : 1.0, respectively. No difference in body size was observed between the males and females. Beetles with the rostrum in the vertical position were 3.0–6.0 (on average 4.9) mm long. Beetles with the rostrum pointing diagonally forward were 3.3–6.3 (on average 5.2) mm long. Interestingly, the average size of their body (incl. rostrum) was gradually decreasing during their emergence from 5.3 mm (in the 1st quarter of eclosion period) to 4.7 mm (in the last quarter of eclosion period). According to literary data, the adults are long from 4 to 6 mm. Corpus adiposum of the freshly emerged beetles is developed only partially and reproductive organs mature only during the maturation feeding.

The beetles seek out leaves budding and freshly budded, especially on young shrubs and coppice shoots of oak trees. They start biting out narrow band-shaped (linear) feeding notches from the adaxial face of the leaf blade that are 2–15 (on average 4.7) mm long and 1–2 (on average 1.3) mm wide. Beetles kept in the laboratory produce feeding notches 5–18 mm long and 1–3 mm wide. At about 90 % they window the leaves and at 10 % they skeletonise them (gnawing down to the lower leaf epidermis, which they leave intact). Bitten out linear patterns consist of minute oblong holes (or mines) whose length equals the band width (i.e. on average 1.3 mm), and whose width ranges from 0.3–0.5 (on average 0.4) mm. Individual feeding notches are arranged close together into straight or slightly curved stripes so that one small feeding notch falls to 1 mm of stripe length. Leaf veins including venular anastomoses are usually not damaged by the beetles.

Frass pellets of the beetles are black, filamentous and mildly strangulated. They are 0.18–1.8 (on average 0.9) mm long and 0.17–0.21 (on average 0.19) mm wide and very readily disintegrate into fragments that are 0.17–0.36 (on average 0.25) mm long. In the laboratory, the beetles produced from 1 cm^2 of damaged leaf blade on average 35 frass pellets the average length and width of which was 0.9 mm and 0.19 mm, respectively. The beetles live two to three months and damage about 30 cm^2 of reduced leaf area by their maturation feeding. In capture, the beetles sometimes browsed the surface of the bark of young oak shoots and sporadically petioles in addition to leaf blades.

The beetles are most active in warm and sunny weather. Cold and rainy weather they wait out hidden under leaves or in various ground hiding places on trees and elsewhere. In favourable (and even windy) weather, they intensively ingest during the day and repeatedly mate on the trees. Copulating beetles can be observed in the open from the end of April to the end of June. In the area of the Vranov forest district, the beetles often formed small groups (of up to five members) on the shoots during the day in the period of the highest activity (i.e. in the first half of May). After several days of feeding, fertilized females started creating leaf rolls and laying eggs in them.

Preparation of Leaves for Rolling

The oak leaf roller develops in leaf rolls and this is why the period of reproduction coincides with the period of leaf rolling. Sexually mature and fertilized females choose for rolling freshly budded leaves of suitable size, shape and consistence. At a distance of 2–4 (on average 3) mm from the contact of subsequent cross cuts with the main vein (in direction towards the leaf blade base), they bite out a transversal mine into the main vein, sized ca. 1.4 × 0.8 mm prior to cutting the leaf. The feeding notch normally reaches down to the lower epidermis and cuts a part of the vein vascular tissues. In a 2–4 mm section between this mine and the contact point of the two cuts, the female often gnaws a fine surface groove of ca. 0.3 mm in width. This typical treatment of the main vein significantly affects leaf blade wilting as well as the later shedding of leaf rolls.

Subsequently, the female bites out two transversal cuts into the punctured leaf (at about a third of its length), leading from the left and the right blade margin up to the main leaf vein. The cuts are in fact long strip-shaped notches 1.0 mm wide, which connect on the main vein in one point. On the lobed leaves of oaks, one of notches normally begins between two neighbouring lobes. This is why this notch is usually shorter than the opposite one, which cuts the leaf lobe from its apex. The notches run ± straightforward and more or less perpendicularly to the main vein, or somewhat arcuately approach the obliquely standing lateral veins (Fig. 1).

The numerous cross cuts (indentations) that the females of *A. nitens* bite out into larger-diameter veins facilitate easier and regular bending of leaf veins (main vein and basal-middle sections of lateral veins in particular) during the later creation of leaf rolls. The most conspicuous and most numerous are indentations on the abaxial (i.e. lower, back) side of the prominent main vein. In its basal half, the indentations are even dual (with a short interruption in the middle of the vein).

The number and location of notches was determined on 50 leaves of *Q. petraea* (average length and width of the rolled leaf blade part 51.6 cm and 29.5 cm, resp.). There were on average 167.3 notches on the abaxial side of the main vein along its length (apart from the thinnest apical part only a few mm long). The notches were close to each other at a distance of 0.3 mm (i.e. three notches per one mm of vein length). On the adaxial (i.e. upper, true) side of the main vein, there were on average 49.5 notches (i.e. by 3.3times less than on the abaxial side of the vein). The notches were at all times simple and occurred namely in the basal and middle part of the vein at a distance of ca. 1.0 mm from one another. Lateral veins were damaged only in their basal halves by on average 90.2 notches on the abaxial side and 44.5 notches on the adaxial side. Out of the total number of 348 notches, the main vein exhibited 61.3 % of notches (of which 47.1 % and 14.2 % were on the abaxial and adaxial side, resp.). On the lateral veins, there were on average 38.7 % notches (of which 25.9 % and 12.8 % were on the abaxial and adaxial side, resp.). On the main veins, a half of the notches on the abaxial side were dual and in total 1.6times more numerous than those on lateral veins. Notches on the lateral veins were at all times simple.

Damage to the leaf blade by irregular superficial notches mentioned e.g. by Francke-Grosmann (1974) was not demonstrated in the Brno region. Various deviations occur from the usual bilateral cross cut connecting on the main leaf vein. For example, the female creates only a unilateral cross cut, which runs through the main vein and ends 5–9 mm from the lateral edge of the leaf blade. The to-be leaf roll (if it is created at all) then hangs on the peripheral blade part reinforced by a sole lateral vein. Sporadically, leaf blades are damaged by two-to-three bilateral cross cuts and two-to-three mines in the main vein. Not plentiful are leaves with unfinished unilateral cross cuts, which sometimes run down to the main vein. Veins on such leaves never feature notches or mines, this indicating that the female gets to the veins only after having cut the blade. According to Formánek (1911), the female can roll a small leaf without a prior making of bilateral cuts. Leaves with this type of damage were not found in the Brno region.

Leaf Rolling and Egg Laying

Females of *A. nitens* living in the Brno region breed from the end of April to mid-July. At the beginning, they lay eggs into rolls on primary annual shoots, from mid-June into rolls on the secondary (so-called Lammas) shoots (Tabs. I and II, Fig. 2). After several hours, the female returns usually at night to the cut wilting leaf and starts rolling it. At first, she folds the wilted part of the leaf along the main leaf vein, adaxial parts facing each other, and lays mostly (83.6 %) one egg and maximally 5 eggs between the two leaf halves. On average, the female lays only 1.1 eggs into one leaf roll. Sporadically, the leaf rolls contain no eggs, this being apparently caused by problems with placing the egg into the leaf blade fold and by subsequent falling of the leaf onto the ground (Tab. III). Literary data concerning the number of eggs in the leaf rolls are in their majority vague and therefore we do not present them here.

Eggs are 0.64–0.96 (on average 0.83) mm long and 0.57–0.75 (on average 0.68) mm wide (Tab. IV, Fig. 3). According to Scherf (1964), the eggs are only 0.5–0.55 mm long and 0.25–0.3 mm wide. Fig. 3 shows that of all compared leaf-rolling weevils the eggs of *A. nitens* are the least slender ones (almost globular). They are yellow, smooth, semi-gloss, rarely dull and slightly sticky at the beginning. Eggs infested by oophagous endoparasitoids are brown. During oviposition, they are fixed to the leaf epidermis by the sticky secretion of accessory glands. A majority of eggs is laid into the fold in the tip of longitudinally folded leaf (up to a distance of max. 1.5 cm, exceptionally up to 3 cm from the leaf apex).

After having laid the eggs, the females begin rolling the two leaf halves (from the tip towards the petiole) into a compact transversal roll, by which the eggs appear in the middle of the leaf roll. The ring-rolled main leaf vein, situated vertically to the longitudinal axis of the leaf roll, strengthens the upper edge of the roll. On the opposite (lower) end, the roll is closed by the folded leaf margins. The result is a cylindrical roll, which remains connected with the unrolled leaf base by means of the fitted main vein. The rolls are 5–17 (on average 8.9) mm long and 4–10 (on average 6.6) mm wide (Tab. V, Fig. 1). The size of leaf rolls on the primary and secondary annual shoots does not show any significant difference. Literary data on the dimensions of leaf rolls are sporadic and biased.

The rolls are made largely at night when the leaf tissues are more flexible (e.g. at dew) and easy to roll. Finished rolls dry out and become hard on sunny days. The females choose only the most suitable current year shoots for reproduction and this is why some shoots remain without rolls even during the pest overpopulation. On the selected shoots, they usually create a higher number of rolls. In the Brno region, there were 1–11 (on average 3.2) leaf rolls on the primary shoots and 1–11 (on average 3.8) leaf rolls on the secondary shoots (Fig. 4). According to Ševyrev (1914), the females roll 5 to 6 leaves on the shoots. On the primary shoots, they damage primarily the terminal leaves, on the secondary shoots they damage mainly the leaves occurring in the half of the shoot length. In the studied area, nearly a third of leaves were damaged by rolling on the primary and secondary shoots (Fig. 5).

The fertility of *A. nitens* females is relatively low. According to Scherf (1964), the females lay approximately 12–20 eggs into 12–14 leaf rolls within 50–70 days. The results of our research showed they lay on average 25 eggs into 23 leaf rolls within a month and a half up to two months and a half. Low fertility (ca. 30 eggs) has also another representative of the Attelabidae family – *Apoderus coryli* (L.) (Urban, 2014). Somewhat higher fertility (ca. 35 eggs) is shown by native representatives of the Rhynchitidae family – *Deporaus betulae* (L.) and *Byctiscus populi* (L.) (Urban, 2012a, 2012b). The highest number of eggs (ca. 50) is laid by the females of *B. betulae* (L.) (Urban, 2015).

Development of Eggs and Larvae

Embryogenesis lasts 2–4 weeks. In the laboratory (and in the open in warm weather during the second half of June and beginning of July), the development is markedly shorter than at relatively low May temperatures (Fig. 2). Larvae of the 1^{st} instar do not consume chorion, and after several hours of “rest” they start ingestion. They bite out tiny feed marks (holes, “windows”) into the wilted parts of the roll without damaging leaf veins and leaf anastomoses. Their head case (cranium) is 0.43–0.54 (on average 0.48) mm wide (Tab. IV, Fig. 6). They are 0.9–3.2 mm long and 0.5–1.2 mm wide. Grown-up larvae of the 1^{st} instar are 2.2–3.2 mm long and 0.9–1.2 mm wide. During the feeding, they produce brown to black filamentous frass pellets, which are 1–2 mm long and 0.036 mm wide. Due to strong cross strangulation, the frass pellets readily disintegrate into sections 0.09–0.25 mm long. In 2–5 weeks, the 1^{st} instar larvae damage 0.2–0.3 cm^2 of the leaf. They come of age in July and in the first half of August and moult within the leaf rolls (Fig. 2).

Larvae of the 2^{nd} instar continue after a short rest in feeding on the inside of the roll. These larvae have the cranium 0.7–0.9 (on average 0.8) mm wide (Tab. IV, Fig. 6). They are 2.6–6.4 mm long and 1.0–2.5 mm wide. Grown-up larvae are 4.0–6.4 mm long (according to Scherf, 1964, they are long 6–8 mm, according to May, 1993 they are long up to 6 mm) and 1.7–2.5 mm wide. Their head is brown and partly retractable into thorax. Thorax and abdomen are yellow up to orange, rarely whitish, with long setae; abdomen segments are compartmentalized by 1–2 transversal grooves. Mandibulae are dark, tridentate, palpi labiales and palpi maxillares consist of two segments. The larvae produce filamentous black frass pellets, which are 1.5–2.5 mm long and their diameter is 0.07–0.1 mm. At the point of strangulation, the frass pellets readily disintegrate into sections that are 0.18–0.36 mm long. During the feeding, the numerous and copious frass pellets fill a great part of the eaten out leaf roll inside. Larvae of the 2nd instar damage 1.5–2.0 cm^2, larvae of both instars damage 1.7–2.3 cm^2 of reduced leaf area. After the end of feeding, cavities eaten out in the rolls are at least twice the size of the larvae. For instance, a leaf roll of 10 mm in length and 6 mm in width contained an oval cavity 8 mm long and 4.5 mm wide with a larva, which was 6.2 mm long and 2.1 mm wide.

Unlike the larvae of the Rhynchitidae family (*D. betulae*, *B. betulae* and *B. populi*), the larvae of the Attelabidae family (*A. nitens* and *A. coryli*) develop through two instars only (Figs. 2, 6) (Urban, 2012a, c, 2014, 2015). The development of *A. nitens* eggs and larvae is however very slow. Larvae emerged in the Brno region from eggs laid from May to the first half of July come of age as late as in September and October. After the end of feeding, they remain in leaf rolls and hibernate in them, pupating always within the rolls in April. Oncoming and course of pupation depend on weather. The stage of pupa lasts 10–17 days (according to Scherf, 1964, 8–11 days). Pupae are limited in motion; they are 3–6 mm long, yellow, with long setae. Beetles emerge towards the end of April and at the beginning of May; they die during July. Eggs occur from the beginning of May to the end of July. In July, eggs and larvae of both instars can be found in the open at the same time (Fig. 2). The generation cycle is univoltine.

The slow development of *A. nitens* larvae (compared to *A. coryli* larvae) is mentioned e.g. by Escherich (1923). The reason for the stagnating development consists likely in the small size of leaf rolls, which rapidly dry out in warm and dry weather. The larvae respond to worse trophic conditions by slowing down even stopping ingestion, by slowing down metabolism and by retarding or even stopping their development. Their normal activity is resumed only after the leaf rolls are sufficiently moistened again by rain, humid air or dew – even if the period of starvation is longer than a month (according to Schaufuss, 1916, allegedly even after more than four months). By this capability of long starvation, the larvae of *A. nitens* markedly differ from the larvae of *A. coryli* as well as from the larvae of other native species of leaf-rolling weevils.

Further Characterization of the Leaf Rolls

The survey of shoots on diverse *Quercus* species with the leaf rolls made by *A. nitens* in the Brno region brought data about creation of the leaf rolls, their abundance, localization and course of falling onto the ground. Primary (spring) shoots with the leaf rolls (average length 13.7 cm) had in 2014 on average 9.8 leaves of which 3.2 (i.e. 32.6 %) were damaged by rolling. Average area of the blade of intact leaves and damaged leaves was 18.0 cm^2 and 13.8 cm^2 (i.e. by 23.3 % smaller), respectively (Tab. I). This indicates that the leaves usually rolled on the primary shoots with relatively large leaves (ca. 18.0 cm^2) were of considerably below-average size.

Secondary (so-called Lammas, summer) shoots normally appear in the Brno region in the second half of June only on fast growing primary current year shoots. These shoots had on average 12.8 leaves of which 3.5 (i.e. 27.3 %) exhibited leaf rolls. Average area of intact and damaged leaves was 14.6 cm^2 and 15.0 cm^2 (i.e. by 2.7 % larger), respectively (Tab. II). Leaves on the secondary shoots (compared to leaves on the primary shoots) were on average by 18.9 % smaller. On the secondary annual shoots with relatively small leaves (ca. 14.6 cm^2), the females were choosing usually leaves of average up to slightly above-average size for rolling. The average area of leaves rolled on the primary shoots (ca. 13.8 cm^2) did not markedly differ from the average area of leaves damaged on the secondary shoots (ca. 15.0 cm^2). For creating leaf rolls on the oak trees, the females of *A. nitens* pick out shoots with the leaves of suitable size (ca. 14.4 cm^2), shape and consistence. If they find such shoots, they normally damage more (max. up to 11) leaves on them.

Out of the total average number of 9.9 leaves on the primary shoots studied in the Brno region, on average 3.1 (i.e. 31.3 %) were rolled. Out of the total average number of 13.2 leaves on the secondary shoots, on average 3.9 (i.e. 29.5 %) were rolled. The average number of leaves on the primary and secondary shoots was increasing with the increasing average leaf area. The percentage of leaves damaged on the primary shoots significantly decreases with the increasing leaf area (Tab. VI). The greater is the length of shoots and the number of leaves on the primary and secondary shoots, the lower is the percentage of damaged leaves (Tab. VII, VIII). The percentage of leaves with rolls rapidly decreases with the increasing length of primary shoots, and the average area of damaged leaves increases (Tab. IX). The average area of both intact and damaged leaves significantly increases with the increasing length of current year shoots (with primary and secondary increment) (Tab. X).

Prior to rolling, the female of *A. nitens* bites through the leaf blade in its basal third up to the main leaf vein, by which the blade is divided into two parts. The length and width of the basal leaf part and rolled middle and apical leaf parts (in dependence on the total area of damaged leaves) are presented in Tab. XI and Fig. 7. Out of the total average area of damaged leaves (14.3 cm^2) only 2.4 cm^2 (i.e. 16.8 %) fall to the unrolled base and 11.9 cm^2 (i.e. 83.2 %) fall to the rolled leaf blade part (Tab. XII). The leaf roll is usually created from the whole part of the blade that has been cut, less frequently only from its part.

The freshly made leaf rolls remain on the trees. Inner tissues in the roll gradually turn brown and black from the blade apex and stay green for a longer time only at the cut. In warm and dry weather, the leaf rolls dry out like hay and become brittle (friable). The bases of damaged leaves stay green during the whole vegetation period though. First rolls start to fall from the trees sporadically as early as at the end of May. In June 2014, about 20 % of leaf rolls fell from the primary and quite surprisingly also from the secondary shoots in the Brno region. The percentage of fallen leaf rolls was increasing during the growing season and in October it reached 48.3 % on the primary shoots and 73.7 % on the secondary shoots (Tabs. XIII, XIV). Primary sections of annual shoots with the secondary increment exhibited only 4.2 % of leaves damaged by the rolls and 42.9 % of them fell off the trees before October (Tab. XIV). Warm, dry and windy weather contributes to fast shedding of the rolls. Before winter (spring), more than 75 % (ca. 95 %) of leaf rolls fall off the trees.

A. nitens needs certain moisture content in leaf tissues inside the rolls for its development. Moisture loss is prevented by walls of the rolls, which are formed by 6–12 (on average 9.3) layers of leaves. At the beginning, drying out of the rolls is restricted also by the temporarily functional main leaf vein. However, the main vein in the leaf roll dies during the first month (due to severe damage by numerous cuts and a deep mine), and the roll starts drying out from the outside. A further fate of larvae in the leaf rolls depends on vertical and horizontal precipitation. Fallen leaf rolls dry out slower and often moulder on the ground in wet weather. However, the partial decomposition of leaf tissues does not represent an obstacle to the successful development of the larvae.

Mortality

The decreasing abundance of *A. nitens* is caused by both abiotic and biotic factors. Daanje (1957) and other authors claim the larvae to be very drought-resistant. Our observations indicate, however, that long-lasting very warm and dry weather may have a considerable regulatory effect. Tropical temperatures and absence of rain in June and July 2014 in the Brno region were responsible for a ca. 20 % increase in the mortality of eggs and 1st instar larvae in leaf rolls on the primary shoots of oak trees growing at extremely warm sites (e.g. in Brno-Žabovřesky and in Brno-Komín). The unfavourable weather reflected also in the increased mortality of 5-year *Quercus robur* (and less also *Q. petraea*) plantations. According to Lengerken (in Scherf, 1964), females mitigate the impact of critical drought by biting off ready-made leaf rolls because larvae sustain drought spells better in leaf rolls fallen onto the ground.

The rolls of *A. nitens* are used for oviposition by *Lasiorhynchites sericeus* (Hbst.) (Rhynchitidae). In the Czech Republic, *L. sericeus* occurs rarely and locally. It was not detected in the rolls of *A. nitens* in the Brno region. According to Voss (1932), the "cuckoo" female of this leaf-rolling weevil is attracted by the smell of the wilting cut leaf. She lays eggs into the rolled leaf (on the boundary between the rolled and unrolled leaf part) or into the ready-made leaf roll. Biting out a small hole in the roll, the female pushes the laid egg into it by means of rostrum and closes the hole by secretion (Prell, 1925). Her eggs differ from the eggs of *A. nitens* by size, greater slenderness and whitish colour. They are 0.65 mm long and 0.3 mm wide (Scherf, 1964). The female lays only one egg (exceptionally two) into the leaf roll (Voss, 1932). Scherf (1964), Kopelke (1983), Szujecki (1983), Stejskal and Trnka (2013) a.o. inform that larvae of the two leaf-rolling weevil species live in the rolls side by side without mutual competition. They consume the wilting and slowly decomposing leaf tissues and pupate as late as in the spring. Nevertheless, Kopelke (1983) mentions a so-called spatial parasitism in this connection, at which the host can be attacked sometimes. The entomophagous behaviour of *L. sericeus* larvae is mentioned for example by Knutelski (2007). This kind of parasitism is rather unique in Coleoptera. An obligatory predator of eggs and frequently cited nest kleptoparasitoid in the leaf rolls of North-American leaf-rolling weevil species from the Attelabidae family is *Pterocolus ovatus* (F.) (family of Rhynchitidae).

Adults of *A. nitens* caught in the period from 24th May to 18th June 2014 in Brno-Žabovřesky and in the Vranov forest district yielded Tachinidae family imagos during June in the laboratory. Grown-up larvae of the tachina fly abandoned their victims and pupated in puparia ca. 3.5 mm long and 1.5 mm wide. These parasitoids infested approximately 40 % of beetles, which considerably complicated the laboratory breeding.

Eggs of *A. nitens* are parasitized by *Poropoea stollwerckii* Först. (Trichogrammatidae) (Nikolskaja, 1952; Subba Rao, 1969; Nikolskaja and Trjapicyn, 1978; Ribes, 2011). According to Silvestri (1916), females of *P. stollwerckii* lay eggs already in the 2nd half of April. Larvae develop through five instars and the development from oviposition to adult individual lasts 14–15 days. However, the actual ingestion period lasts only a few days. In Italy, *P. stollwerckii* has two generations in the eggs of *A. nitens* (Clausen, 1940). Grown-up larvae of the second generation persist in the host's eggs from June until the spring when they pupate in them. The parasitoid may be of great significance in reducing the abundance of *A. nitens* since it can destroy over 50 % of its eggs (Silvestri, 1916). According to Daanje (1957), the pre-preparation of leaves for rolling reflects in the short time of creating leaf rolls and hence in the lower infestation of eggs.

P. stollwerckii is apparently of little regulatory importance in the Brno region. 1,165 rolls harvested in the open in 2014 (and transferred into the laboratory on 1th April 2015) yielded only 19 wasps (parasitization 1.6 %) from 10th–21th April. From the territory of the former Czechoslovakia, *P. stollwerckii* was observed to occur only in Moravia (Kalina, 1989). *P. defilippii* Silv. (Hoffmann, 1958;

Scherf, 1964) and *Ophineurus signatus* Ratz. (Scherf, 1964) develop in the eggs of *A. nitens* too. These two species and *P. minkiewiczi* Now. parasitize also in eggs of the abundant polyphagous *Byctiscus betulae* (L.). Representatives of the oophagous Trichogrammatidae family belong in the Czech Republic to natural regulators of the abundance of distinctive leaf-rolling weevil species (Urban, 2012a, b, c, 2014, 2015).

From mid-July, whitish rolls of parasitoids were observed in leaf rolls with dead *A. nitens* larvae in the Brno region, which were 2.5–3.5 mm long and 1–2 mm wide. In the spring of 2015, 1 165 last year's leaf rolls of *A. nitens* yielded 21 imagos from the Braconidae family (parasitization 1.8 %) and one imago from the Ichneumonidae family (parasitization 0.1 %). According to Hoffmann (1958), parasitoids of oak leaf roller include *Diaspilus capito* Nees (Braconidae) and *Elachertus idomene* (Walk.) (Eulophidae).

Common inhabitants of *A. nitens* leaf rolls in the Brno region are saprophagous and occasionally saproparasitoid larvae of Cecidomyiidae. The orange-red Cecidomyiidae larvae (long 0.7–2.0 mm) were found in about 10 % of leaf rolls in the period from mid-June to the end of the growing season. The leaf rolls usually contained more (max. up to 15) larvae. Sucking larvae were observed several times on eggs, once on a 1st instar larva. Caterpillars of Lepidoptera damaged about 5 % of leaf rolls on the primary and secondary shoots, and in a greater part of damaged rolls, *A. nitens* was destroyed.

Young leafed shoots on shrubby oaks and young coppice shoots are in the Brno region often grazed by roe deer (*Capreolus capreolus* /L./). In the Vranov forest district, ¾ of *A. nitens* leaf rolls on coppice shoots were liquidated by roe deer browsing at the end of May and beginning of June 2014. By 28 May, for example a total number of 56 coppice shoots (average length 45 cm) grew up from a stump of 50 cm in diameter. Most coppice shoots featured 1–6 (on average 4) rolls. Only on this stump, the roe deer consumed 106 of 146 leaf rolls (i.e. 73 %). In the Vranov forest district, *C. capreolus* intensively damaged also leaves in the ground parts of *Castanea sativa* crowns. At all times, the game grazed on the distal half of leaves, which reminded damage by *A. nitens* females at the first sight. Game damage to leaves can be discerned from *A. nitens* damage by uneven cuts and absence of leaf rolls.

During the vegetative rest, insectivorous birds for which the larvae are a sought delicacy peck up the unshed leaf rolls of *A. nitens*. This is why the larvae hibernating in the leaf rolls on trees have only a low probability of successful winter survival. However, the regulatory activity of birds is impaired by the fact that a majority (more than 75 %) of leaf rolls falls off the trees before the beginning of winter.

Mortality of eggs and larvae of *A. nitens* in leaf rolls on primary and secondary shoots of *Quercus* spp. in the Brno region during the period from April to October is illustrated in Tabs. XV and XVI. The tables show that leaf rolls on the primary shoots exhibited on average 36 % of dead individuals (of which 15 % were eggs, 16 % were1st instar larvae and 5 % were 2nd instar larvae). Leaf rolls on the secondary shoots featured on average 28 % of dead individuals (of which 22 % were eggs, 5 % were 1st instar larvae and 1 % were 2nd instar larvae). The highest mortality was detected in tiny rolls with the below-average leaf area rolled (Tab. XVII). The increased mortality of *A. nitens* eggs and larvae in the small leaf rolls apparently relates to lower protection from unfavourable abiotic factors and some biological enemies.

Economic Importance

Oak leaf roller (*A. nitens*) is an abundant and widely spread West Palaearctic species most frequently occurring on *Quercus* spp. and on *Castanea sativa*. Females create cylindrical rolls of leaf blades, which they pre-treat and bite crosswise into two parts prior to rolling. Most infested are young trees from natural and artificial regeneration (up to 3 m in height) and coppice shoots. Overpopulated, they can damage more than 50 % of leaves (Francke-Grosmann, 1974) or nearly all of them (Escherich, 1923). For example Lampert (1909), Schaufuss (1916), Živojinovič (1948), Gusev and Rimskij-Korsakov (1953), Vasiljev *et al.* (1975), Goloverda and Mozoľ (1977), Gogola *et al.* (1998), Wilkie (2010), Kalapanida and Petrakis (2012) and other authors take the species for a pest on young oak trees. On *C. sativa*, the beetles may damage flower buds by their maturation feeding (Juhásová *et al.*, 2010). A mass attack looks like damage by late frost (Pfeffer *et al.*, 1961) or fire (Marre, 1916).

Similarly as *Apoderus coryli* (L.) and *Deporaus betulae* (L.), females of *A. nitens* never cause harm to shoots themselves. This is why the economic importance of *A. nitens* (as compared with *Byctiscus betulae* /L./ and *B. populi* /L./) is much lower even if nearly all leaves are damaged by the rolls. The pest usually needs no control. Some authors sporadically recommend the collection of leaf rolls (Živojinovič, 1948) or the application of insecticides (Goloverda and Mozoľ, 1977).

I: *Basic characteristics of primary ("spring") shoots on Quercus spp. and their damage by leaf rolls produced by Attelabus nitens. Brno region, 2014*

Date	Locality-Species	Number of shoots	Average length of shoots (cm)	Average number of leaves/ of these damaged	Percentage of damaged leaves	Average area of intact/ damaged leaves (cm²)	Difference (cm²/%)
30th April	Kamenný vrch- *Q. pet.*	1	25.0	12.0/4.0	33.3	26.9/16.9	-10.0/37.2
7th May	Vranov- *Q. pet.*	11	14.0	9.5/2.3	24.2	17.8/15.9	-1,9/10.7
10th May	Brno-Komín- *Q. pet.*	3	25.0	10.0/4.0	40.0	28.1/16.9	-11.2/39.9
14th May	Vranov- *Q. dal.*	7	22.6	12.0/2.7	22.5	25.0/19.1	-5.9/23.6
17th May	Brno-Žabovřesky- *Q. pet.*	4	5.0	6.8/1.3	19.1	11.2/15.5	+4.3/38.4
21th May	Vranov- *Q. dal.*	6	15.0	11.0/3.2	29.1	21.9/18.0	-3.9/17.8
24th May	Brno-Žabovřesky- *Q. rob.*	2	8.5	10.5/1.0	9.5	11.2/15.0	+3.8/33.9
28th May	Vranov- *Q. dal.*	11	15.4	10.2/4.3	42.2	16.8/15.5	-1.4/8.3
31th May	Brno-Komín- *Q. rob.*	5	7.8	9.4/3.2	34.0	18.4/20.3	+1.9/10.3
4th June	Vranov- *Q. dal.*	9	22.2	13.7/3.2	29.9	23.7/12.5	-11.2/47.3
7th June	Brno-Komín- *Q. pet.*	7	11.6	11.1/2.6	23.4	12.1/12.8	+0.7/5.8
11th June	Vranov- *Q. dal.*	6	10.5	8.8/4.7	53.4	10.0/12.2	+2.2/22.0
14th June	Brno-Žabovřesky- *Q. pet.*.	9	10.3	9.3/2.9	31.2	17.0/12.4	-4.6/27.1
18th June	Vranov- *Q. dal.*	6	15.2	9.7/4.2	43.3	13.8/13.0	-0.8/5.8
22th June	Brno-Komín- *Q. rob.*	4	10.2	8.5/2.3	27.1	20.1/13.1	-7.0/34.8
25th June	Vranov- *Q. dal.*	6	10.7	9.2/4.2	45.6	12.4/11.3	-6.3/36.4
29th June	Brno-Komín- *Q. pet.*	8	13.4	10.0/3.4	34.0	17.1/16.1	-1.0/5.8
2th July	Vranov- *Q. pet.*	6	8.8	7.0/3.3	47.1	12.5/13.2	+0.7/5.6
8th July	Horákov- *Q. pet.*	6	15.0	12.8/3.7	28.9	13.9/14.0	+0.1/0.7
12th July	Červený kopec- *Q. rob.*	8	4.4	6.9/2.3	33.3	22.3/15.0	-7.3/32.7
15th July	Bílovice n. Sv.-*Q. pet.*	2	16.0	12.5/5.0	40.0	17.1/14.2	-2.9/17.0
22th July	Vranov- *Q. pet.*	6	13.7	10.2/2.5	24.5	17.9/10.2	-7.7/43.0
28th July	Vranov- *Q. pet.*	6	15.0	8.7/3.7	42.5	22.1/15.9	-6.2/28.0
4th Aug.	Vranov- *Q. pet.*	7	20.4	11.7/3.6	30.8	18.5/13.8	-4.7/25.4
11th Aug.	Vranov- *Q. pet.*	7	14.7	8.4/3.0	35.7	19.1/14.1	-5.0/26.2
18th Aug.	Vranov- *Q. pet.*	8	14.9	9.8/3.9	39.8	23.6/14.3	-9.3/39.4
18th Aug.	Velký Hornek- *Q. pub.*	7	11.3	8.9/2.0	22.5	13.5/13.2	-0.3/2.2
25th Aug.	Vranov- *Q. pet.*	7	13.6	9.3/3.7	39.8	15.5/8.4	-7.1/45.8
1th Sept.	Vranov- *Q. pet.*	7	15.0	9.1/3.0	33.0	13.5/10.6	-2.9/21.5
8th Sept.	Vranov- *Q. pet.*	7	12.4	9.1/3.1	34.1	10.0/9.7	-0.3/3.0
15th Sept.	Vranov- *Q. pet.*	7	12.0	11.7/3.4	29.1	19.5/9.7	-9.8/50.3
22th Sept.	Horákov- *Q. pet.*	7	17.0	10.9/3.7	33.9	19.6/12.2	-7.4/37.8
29th Sept.	Vranov- *Q. pet.*	7	10.7	8.6/2.1	24.4	22.6/9.0	-13.6/60.2
6th Oct.	Podkomorské lesy-*Q. pet.*	7	11.9	8.6/2.7	31.4	14.0/11.1	-2.9/20.7
Total (average)		**217**	**13.7**	**9.8/3.2**	**32.6**	**18.0/13.8**	**-4.2/23.3**

Legend: *Q. pet.* – *Quercus petraea*, *Q. dal.* – *Q. dalechampii*, *Q. rob.* – *Q. robur*, *Q. pub.* – *Q. pubescens*.

II: *Basic characteristics of current year shoots on Quercus spp. with primary and *secondary ("Lammas") increment and their damage by leaf rolls produced by A. nitens. Brno region, 2014*

Date	Locality-Species	Number of shoots	Average length of shoots (cm)	Average number of leaves/ of these damaged	Percentage of damaged leaves	Average area of intact/ damaged leaves (cm^2)	Difference (cm^2/%)
18th June	Vranov- *Q. dal.*	3	22.7	14.7/-	-	16.3/-	-
			*24.7	15.3/4.7	30.7	12.6/12.2	-0.4/3.2
22th June	Brno-Soběšice- *Q. pet.*	3	29.3	15.3/-	-	38.1/-	-
			*45.3	16.6/3.0	18.1	23.3/21.8	-1.5/6.4
25th June	Vranov- *Q. dal.*	6	18.3	11.2/0.2	1.8	17.3/11.0	-6.3/36.4
			*18.2	11.5/3.5	30.4	12.5/13.1	+0.6/4.8
2th July	Vranov- *Q. pet.*	6	22.5	12.2/-	-	15.5/-	-
			*23.3	13.8/4.8	34.8	24.4/18.8	-5.6/23.0
8th July	Horákov- *Q. pet.*	7	23.6	14.3/0.03	0.2	24.6/20.0	-4.6/18.7
			*23.3	15.1/2.3	15.2	17.9/16.4	-1.5/8.4
15th July	Bílovice n. Sv.-*Q. pet.*	8	14.5	10.4/0.02	0.2	25.4/15.0	-10.4/40.9
			*19.3	12.2/3.0	24.6	12.9/15.6	+2.7/20.9
22th July	Vranov- *Q. dal.*	8	17.2	11.0/0.03	0.3	18.6/12.0	-6.6/35.5
			*10.8	9.5/4.1	43.2	11.4/18.3	+6.9/60.5
28th July	Vranov- *Q. pet.*	8	22.7	13.9/0.07	0.5	27.0/16.6	--10.4/38.5
			*17.5	12.5/3.9	31.2	12.5/13.8	+1.3/10.4
4th Aug.	Vranov- *Q. pet.*	7	18.9	10.7/0.1	0.9	28.4/25.9	-2.5/8.8
			*19.9	14.1/4.4	31.2	14.3/17.9	+3.6/25.2
11th Aug.	Vranov- *Q. pet.*	7	19.4	13.3/0.03	0.2	18.1/5.1	-13.0/71.8
			*17.0	10.7/1.9	17.8	10.5/12.0	+1.5/14.3
18th Aug.	Vranov- *Q. pet.*	7	23.9	13.0/0.08	0.6	27.8/10.5	-17.3/62.2
			*20.1	13.1/4.1	31.3	13.6/11.7	-1.9/14.0
25th Aug.	Vranov- *Q. pet.*	7	22.0	12.7/-	-	25.8/-	-
			*15.1	12.3/4.6	37.4	15.0/15.1	+0.1/0.7
1th Sept.	Vranov- *Q. pet.*	7	25.0	15.6/0.04	0.3	19.4/13.0	-6.4/33.0
			*21.6	15.0/4.0	26.7	9.3/13.4	+4.1/44.1
8th Sept.	Vranov- *Q. pet.*	7	19.9	11.4/0.04	0.3	22.1/7.1	-15.0/67.9
			*18.4	12.4/3.3	26.6	13.2/11.6	-1.6/12.1
15th Sept.	Vranov- *Q. pet.*	7	18.6	11.9/-	-	27.0/-	-
			*24.6	12.4/3.1	25.0	18.7/15.6	-3.1/16.6
22th Sept.	Horákov- *Q. pet.*	7	19.1	12.6/0.6	4.8	15.4/18.0	+2.6/16.9
			*21.1	14.0/2.9	20.7	11.9/9.7	-2.2/18.5
29th Sept.	Vranov- *Q. pet.*	7	17.0	10.1/-	-	22.0/-	-
			*19.7	10.4/3.3	31.7	13.5/12.8	-0.7/5.2
6th Oct.	Podkomorské lesy-*Q. pet.*	7	21.0	13.0/0.14	1.1	30.6/21.0	-9.6/31.4
			*21.4	14.1/2.4	17.0	16.4/11.9	-4.5/27.4
Total (average)		**119**	**20.5**	**12.5/0.08**	**0.6**	**23.2/16.0**	**-7.2/31.0**
			***20.1**	**12.8/3.5**	**27.3**	**14.6/15.0**	**+0.4/2.7**

Legend: *Q. dal.= Quercus dalechampii*, *Q. pet.= Q. petraea.*

III: *Average area of leaves rolled on Quercus spp. (by the number of A. nitens eggs in the rolls). Regarding cannibalism and predation, leaf rolls were assessed only from 30th April to 28th July (primary shoots) and from 18th July to 1th September (secondary shoots). Brno region, 2014*

Number of eggs in the roll	Primary shoots		Secondary shoots		Total	
	Number of shoots/ %	Average leaf area rolled (cm^2)	Number of shoots/ %	Average leaf area rolled (cm^2)	Number of shoots/ %	Average leaf area rolled (cm^2)
0	8/2.4	9.1	5/2.3	10.2	13/2.4	9.5
1	280/83.6	11.8	202/92.7	12.9	482/87.2	12.3
2	42/12.5	13.9	8/3.7	11.3	50/9.0	13.5
3-5	5/1.5	11.8	3/1.3	9.0	8/1.4	10.6
Total	**335/100.0**	**12.0**	**218/100.0**	**12.7**	**553/100.0**	**12.3**
Average number of eggs	**-**	**1.14**	**-**	**1.05**	**-**	**1.1**

IV: *Length and width of vital eggs, and head case width of A. nitens 1st and 2nd instar larvae (in divisions) (1 division = 0.0357 mm). Brno region, 2014*

Dimensions (divisions)	Number/ % of eggs		Number/ % of larvae	
	by length	by width	1st instar by head case width	2nd instar by head case width
12	-		10/5.0	-
13	-	-	107/53.0	-
14	-	-	78/38.6	-
15	-	-	7/3.4	-
16	-	3/1.3	-	-
17	-	23/9.9	-	-
18	2/0.9	48/20.7	-	-
19	5/2.2	66/28.5	-	-
20	12/5.2	81/34.9	-	9/4.9
21	19/8.2	11/4.7	-	30/16.2
22	39/16.8	-	-	64/34.6
23	50/21.6	-	-	54/29.2
24	41/17.6	-	-	22/11.9
25	40/17.2	-	-	6/3.2
26	14/6.0	-	-	-
27	10/4.3	-	-	-
Total	**232/100.0**	**232/100.0**	**202/100.0**	**185/100.0**
Average	**23.3**	**19.0**	**13.4**	**22.4**

V: *Dimensions of A. nitens leaf rolls on the primary and secondary shoots of Quercus spp. Average leaf area rolled in leaf rolls on primary (secondary) shoots was 11.6 cm² (12.3 cm²). 20% of leaf rolls featured a filamentous process ("tag") on their apical end, 2–12 (on average 5.3 mm) long, formed by creased lobed leaf margins. Brno region, 30th April – 6th October 2014*

Length/ Width of leaf rolls (mm)	Number of leaf rolls (by their length) on			Number of leaf rolls (by their width) on		
	primary shoots	secondary shoots	total	primary shoots	secondary shoots	total
4	-	-	-	8	1	9
5	3	1	4	78	19	97
6	38	9	47	162	88	250
7	107	39	146	156	106	262
8	108	60	168	53	44	97
9	90	55	145	18	15	33
10	61	40	101	2	3	5
11	32	28	60	-	-	-
12	21	23	44	-	-	-
13	9	16	25	-	-	-
14	2	2	4	-	-	-
15	3	3	6	-	-	-
16	2	-	2	-	-	-
17	1	-	1	-	-	-
Total	**477**	**276**	**753**	**477**	**276**	**753**
Average (mm)	**8.6**	**9.3**	**8.9**	**6.5**	**6.8**	**6.6**

VI: *Intensity of damage to the leaves of Quercus spp. by A.nitens females on primary and secondary shoots (according to leaf area). Brno region, 7th May–6th October 2014*

Leaf area (cm²)	Leaves on primary/secondary shoots			
	average area (cm²)	average number of leaves	of these damaged leaves	% of damaged leaves
≥ 10	8.7/8.9	7.9/11.8	3.1/3.5	39.2/29.7
11-15	13.0/12.7	9.4/13.9	3.3/4.4	35.1/31.7
16-20	17.9/17.7	10.8/14.3	3.4/3.6	31.5/25.2
≤ 21	27.9/25.8	12.4/13.2	2.7/3.6	21.8/27.3
Total average	**15.6/15.0**	**9.9/13.2**	**3.1/3.9**	**31.3/29.5**

VII: *Intensity of damage to the leaves of Quercus spp. by A. nitens females on primary and secondary shoots (according to shoot length). Brno region, 7th May–6th October 2014*

Shoot length (cm)	Average number of leaves on primary/secondary shoots		% of damaged leaves
	total	of these damaged	
≥ 10	7.4/7.8	2.8/2.9	37.8/37.2
11-20	10.3/11.8	3.4/4.0	33.0/33.9
≤ 21	14.6/15.5	3.6/4.0	24.6/25.8
Total average	**9.9/13.2**	**3.1/3.9**	**31.3/29.5**

VIII: *Intensity of damage to the leaves of Quercus spp. by A. nitens females on primary and secondary shoots (according to the number of leaves on shoots). Brno region, 7th May–6th October, 2014*

Number of leaves on shoots	Average number of leaves on primary/secondary shoots		% of damaged leaves
	total	of these damaged	
≥ 10	7.7/7.8	2.8/3.6	36.4/46.2
11-15	12.5/13.1	3.7/4.1	29.6/31.3
≤ 16	17.9/18.0	3.2/3.9	17.9/21.7
Total average	**9.9/13.2**	**3.1/3.9**	**31.3/29.5**

IX: *Relation between the length of primary shoots, percentage of leaves damaged by leaf rolls of A. nitens and the average area of intact and damaged leaves on Quercus spp. Brno region, 7th May–6th October 2014*

Shoot length (cm)	Number/percentage of leaves			Average area of leaves (cm²)		
	intact	damaged	Total	intact	damaged	Total
≥ 10	435/68.1	204/31.9	639/100.0	13.1	13.0	13.0
11-20	467/71.6	185/28.4	652/100.0	16.0	13.6	15.3
≤ 21	416/81.4	95/18.6	511/100.0	23.2	16.5	22.0
Total (average)	**1318/73.1**	**484/26.9**	**1 802/100.0**	**17.3**	**13.9**	**16.4**

X: *Average leaf area of Quercus spp. in dependence on the shoot length (primary + secondary increment) and on the incidence of A. nitens leaf rolls; primary ("spring") leaves are in numerator, secondary ("summer", "Lammas") leaves are in denominator. Brno region, 18th June–6th October 2014*

Shoot length (cm)	Average leaf area (primary/secondary increment) (cm²)			
	intact	damaged	intact/damaged	Total
≥ 10	15.1/13.6	13.7/14.6	15.1/13.9	14.6
11-20	21.0/12.4	18.0/14.7	20.9/13.0	17.8
≤ 21	26.1/17.5	19.2/15.1	26.0/17.0	21.6
Average	23.1/15.7	17.8/14.9	23.0/15.5	19.7
Total average	**20.2**	**15.2**	**19.7**	-

XI: *Length and width of leaf parts unrolled and usually rolled by A. nitens females on Quercus spp. (according to the total area of damaged leaves); results of examining damaged leaves on the primary shoots are in numerator and on secondary shoots in denominator. Brno region, 30th April–6th October 2014*

Total leaf area (cm²)	Length (mm)		Width (mm)	
	unrolled leaf base	usually rolled leaf part	unrolled leaf base	usually rolled leaf part
≥ 10	9.8/10.2	43.2/49.4	13.8/13.9	24.1/22.6
11-15	13.1/15.0	52.4/54.9	17.7/18.2	30.8/28.0
16-20	19.6/20.8	58.3/62.5	23.6/25.1	35.8/33.7
≤ 21	29.9/25.9	66.1/68.6	35.2/34.4	45.0/43.1
Total	**15.2/17.0**	**52.0/57.7**	**19.5/21.5**	**31.1/30.5**

XII: *Damage to leaf blade on Quercus spp. by A. nitens females prior to rolling. Leaf blade is divided into the unrolled (basal) part and the part that is usually (at 98%) rolled (middle and apical). Results of examining shoots without secondary increment are in numerator, results of examining secondary shoots are in denominator. A total number of 494 damaged leaves on primary shoots were examined in the period from 30th April to 6th October. A total number of 264 damaged leaves on secondary shoots were examined in the period from 18th June to 6th October. Brno region, 2014*

Shoot length (cm)	Average area of damaged leaves (cm²)			
	unrolled part	part usually rolled	unrolled part + part usually rolled	total
≥ 10	2.1/2.5	10.9/12.1	13.0/14.6	13.2
11-20	2.1/2.5	11.6/12.1	13.7/14.6	14.0
≤ 21	3.0/2.8	13.2/12.4	16.2/15.2	15.7
Average (cm²)	2.3/2.6	11.6/12.3	13.9/14.9	14.3
(%)	16.5/17.4	83.5/82.6	100.0/100.0	-
Total average (cm²)	**2.4**	**11.9**	**14.3**	-
(%)	**16.8**	**83.2**	**100.0**	-

XIII: *Damage to primary shoots on Quercus spp. by A. nitens females and the percentage of shed leaf rolls. Brno region, 11th June–6th October 2014*

Month	Number of examined shoots	Average shoot length (cm)	Average number of leaves per shoot	% of damaged leaves	% of shed leaf rolls
June	82	9.6	8.1	45.7	18.9
July	69	10.7	8.4	31.0	24.1
August	87	12.7	9.0	31.1	44.7
September	85	13.1	9.5	31.6	40.0
October	15	12.1	9.3	31.2	48.3
Total	**338**	**(11.6)**	**(8.8)**	**34.1**	**(33.3)**

XIV: *Damage by A. nitens females to leaves on annual shoots of Quercus spp. (according to primary and secondary increment) and the percentage of shed leaf rolls. Brno region, 18th June–6th September 2014*

Month	Number of examined shoots	Primary increment				Secondary ("Lammas") increment			
		average length of shoots (cm)	average number of leaves per shoot	% of damaged leaves	% of shed leaf rolls	average length of shoots (cm)	average number of leaves per shoot	% of damaged leaves	% of shed leaf rolls
June	18	17.7	11.3	6.2	14.3	16.3	10.7	27.1	20.7
July	62	17.2	11.0	3.6	15.0	17.7	12.1	26.4	25.0
August	54	20.6	12.3	5.7	42.8	17.3	11.5	30.4	45.7
Sept.	69	21.0	12.3	2.4	56.7	22.6	13.3	26.3	48.6
Oct.	9	22.1	13.1	5.3	42.9	19.2	12.7	15.0	73.7
Total	**212**	**(19.6)**	**(11.9)**	**4.2**	**(34.0)**	**(19.1)**	**(12.2)**	**27.0**	**(39.4)**

XV: *Incidence and mortality of A. nitens eggs and larvae in leaf rolls on the primary shoots of Quercus spp. Brno region, 2014*

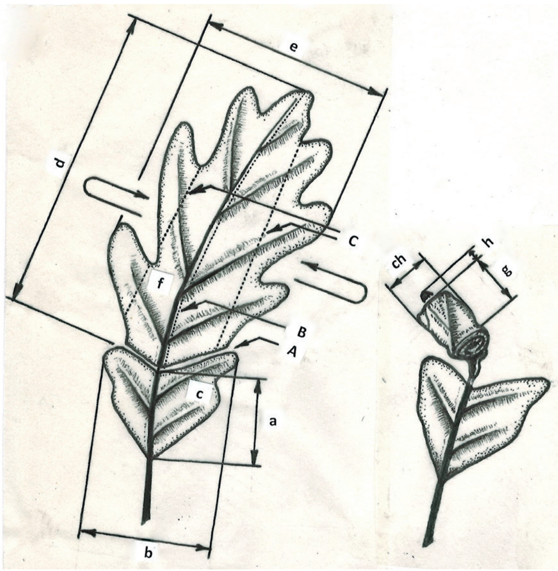
Month	Number of live/dead individuals				Percentage of live/dead individuals			
	eggs	1st instar larvae	2nd instar larvae	total	eggs	1st instar larvae	2nd instar larvae	total
April	4/-	-	-	4/-	100.0/-	-	-	100.0/-
May	129/3	4/-	-	133/3	94.9/2.2	2.9/-	-	97.8/2.2
June	45/5	105/12	-	150/17	26.9/3.0	62.9/7.2	-	89.8/10.2
July	1/6	27/15	18/1	46/22	1.5/8.8	39.7/22.1	26.4/1.5	67.6/32.4
August	-/10	2/8	30/3	32/21	-/18.9	3.8/15.1	56.6/5.6	60.4/39.6
Sept.	-/7	-/10	40/3	40/20	-/11.6	-/16.7	66.7/5.0	66.7/33.3
Oct.	-/1	-	9/-	9/1	-/10.0	-	90.0/-	90.0/10.0
Total	**179/32**	**138/45**	**97/7**	**414/84**	**(36.0/6.4)**	**(27.7/9.0)**	**(19.5/1.4)**	**(83.2/16.8)**

XVI: *Incidence and mortality of A. nitens eggs and larvae in leaf rolls on the secondary shoots of Quercus spp. Brno region, 2014*

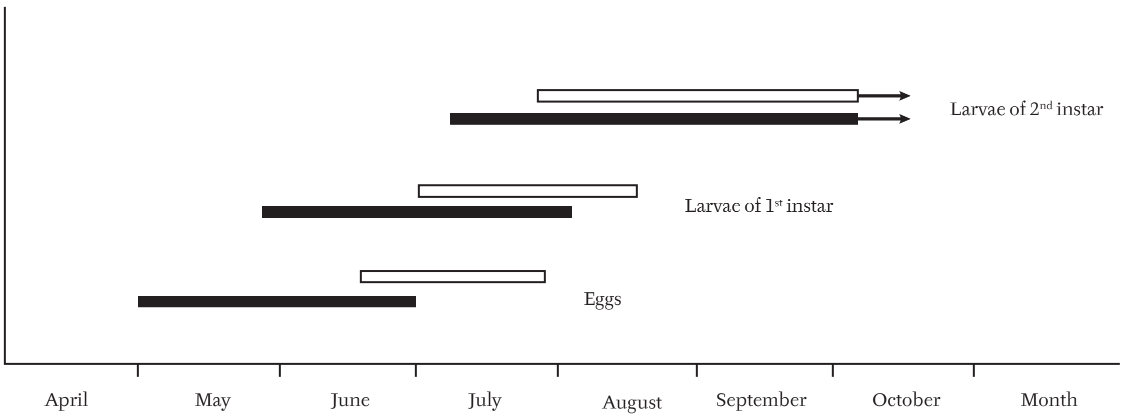
Month	Number of live/dead individuals				Percentage of live/dead individuals			
	eggs	1st instar larvae	2nd instar larvae	total	eggs	1st instar larvae	2nd instar larvae	total
June	31/-	-	-	31/-	100.0/-	-	-	100.0/-
July	22/8	55/4	5/-	82/12	23.4/8.5	58.6/4.3	5.3/-	87.2/12.8
August	-/11	9/6	33/1	42/18	-/18.3	15.0/10.0	55.0/1.7	70.0/30.0
Sept.	-/14	-/3	47/1	47/18	-/21.5	-/4.6	72.3/1.6	72.3/27.7
Oct.	-/1	-	3/-	3/1	-/25.0	-	75.0/-	75.0/25.0
Total	**53/34**	**64/13**	**88/2**	**205/49**	**(20.9/13.4)**	**(25.2/5.1)**	**(34.6/0.8)**	**(80.7/19.3)**

XVII: *Mortality of A. nitens eggs and larvae in leaf rolls on the primary and secondary shoots of Quercus spp. (according to the size of rolled leaf area). Brno region, 4th June – 6th October 2014*

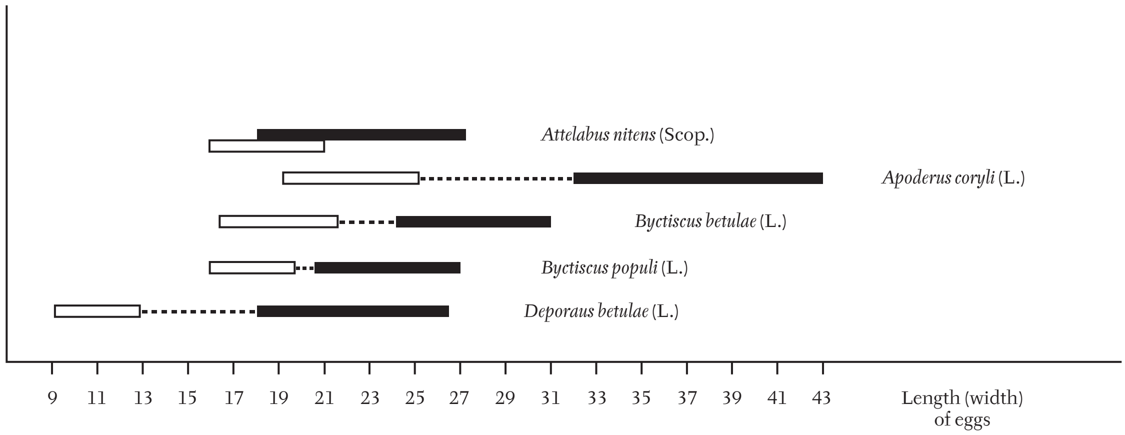
Rolled leaf area (cm^2)	Number/percentage of individuals		
	live	dead	total
≤ 10	205/70.2	87/29.8	292/100.0
11-15	173/79.4	45/20.6	218/100.0
≥ 16	78/79.6	20/20.4	98/100.0
Total	**456/75.0**	**152/25.0**	**608/100.0**



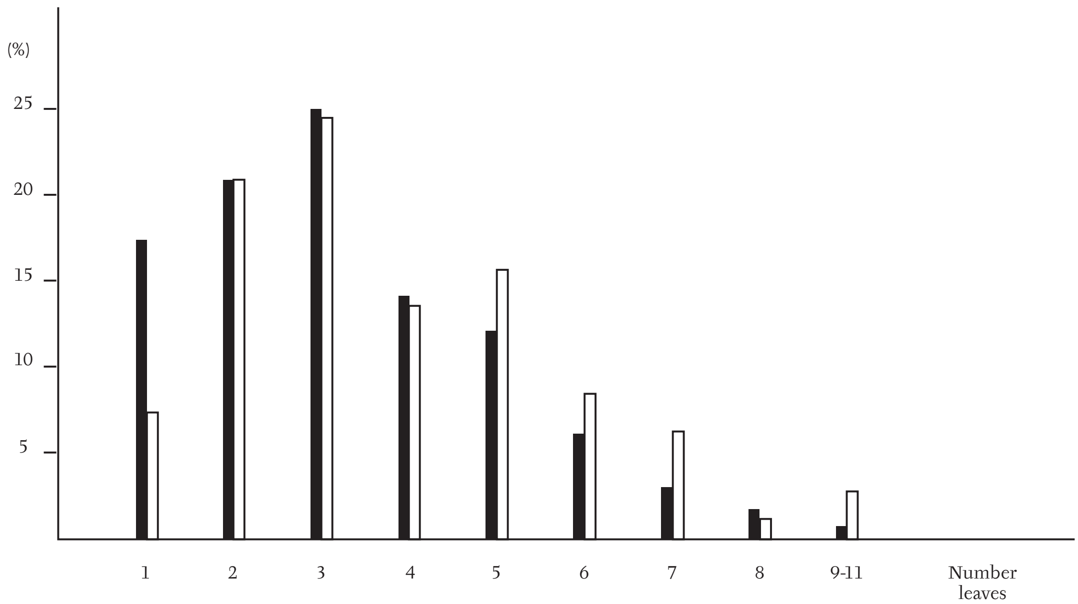
1: *Scheme of a cross cut through the leaf blade of Quercus spp., made by the female of Attelabus nitens (left) and the leaf roll (right). A – cut through the leaf blade, B – line of the blade longitudinal folding on the adaxial side, C – line of the fold of marginal leaf blade parts. Measured values: a, b, c – length, width and area of the leaf blade basal part, d, e, f – length, width and area of the rolled leaf blade part, g – leaf roll length, h – length of terminal tag, ch – leaf roll width.*



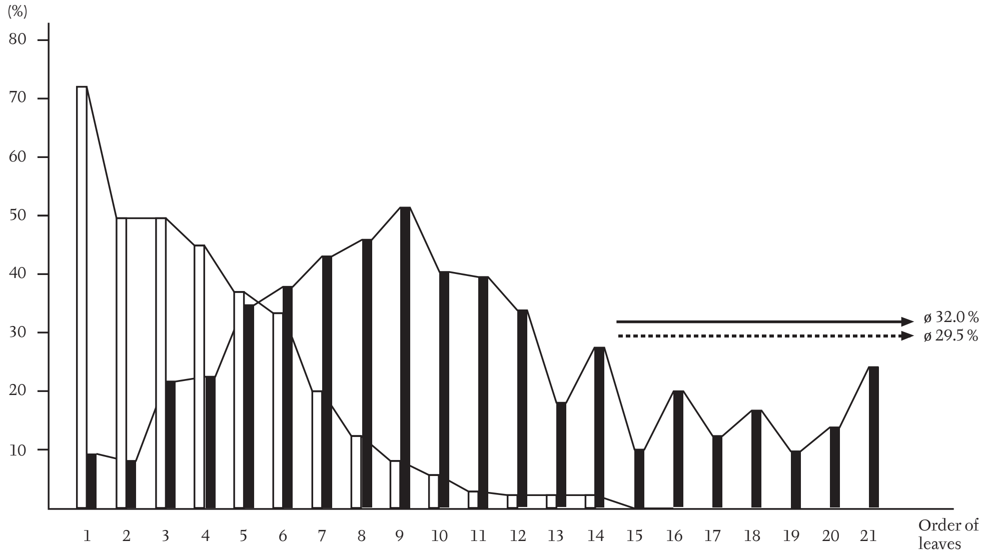
2: *Incidence of A. nitens eggs and larvae in leaf rolls on Quercus spp. Incidence on primary shoots (dark), incidence on secondary ("Lammas") shoots (light). Brno region, 2014.*



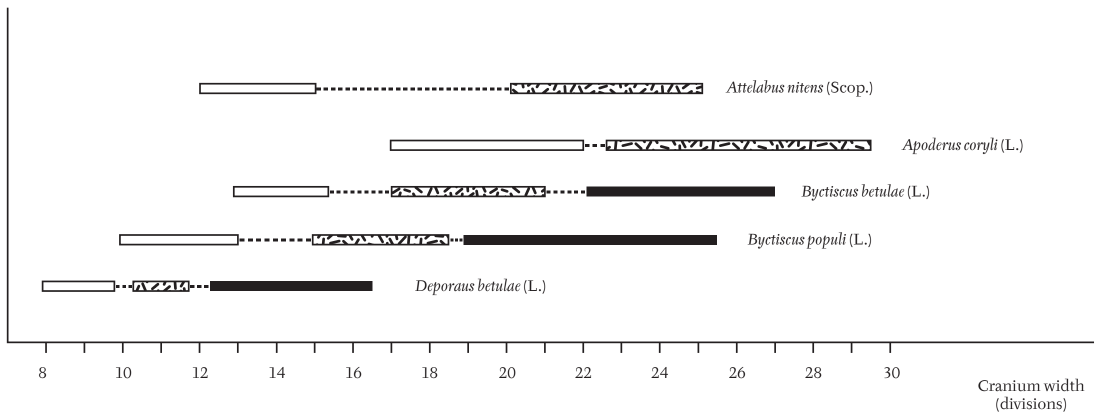
3: *Dimensions of vital eggs (length dark, width light) of A. nitens and other four species of Rhynchitidae and Attelabidae (1 division = 0.0357 mm).*



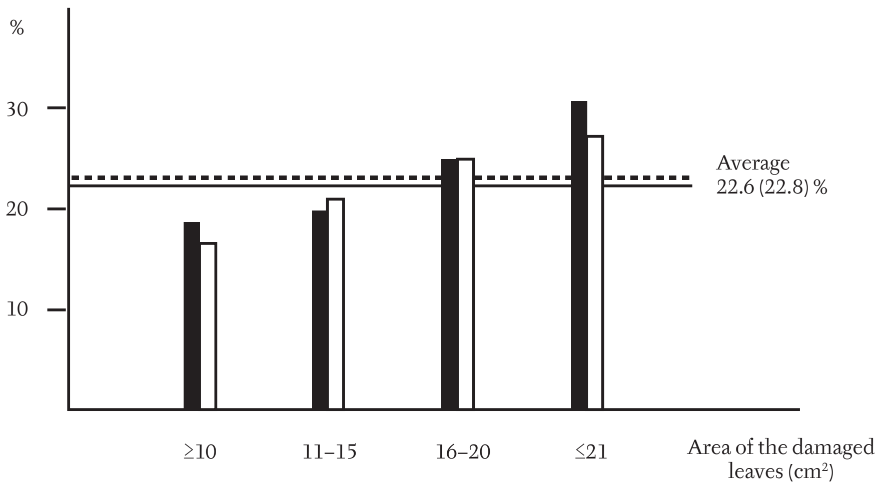
4: *Relative representation of leaves on Quercus spp., damaged by females of A. nitens (according to the number of damaged leaves on primary /dark/ and secondary /light/ shoots). Total number of examined primary shoots was 227 (average number of damages 3.2 per shoot); total number of examined secondary shoots was 110 (average number of damages 3.8 per shoot). Brno region, 7th May–6th October 2014.*



5: *Relative incidence of A. nitens rolls on the leaves of primary (light) and secondary (dark) shoots (according to order from the terminal bud). Average percentage of leaves damaged on primary (secondary) shoots was 32.0% (29.5%). Brno region, 7th May–6th October 2014.*



6: *Head case width in individual instars of the larvae of A. nitens and other four species of Rhynchitidae and Attelabidae (1 division = 0.0357 mm) – 1st instar larvae light, 2nd instar larvae dashed, 3rd instar larvae dark.*



7: *Length of basal (unrolled) leaf blade part on Quercus spp. (in percentage of total leaf length) according to leaf area. Values ascertained on primary (secondary) shoots are marked in dark (light). Brno region, 7th May–6th October 2014.*

SUMMARY

Attelabus nitens is an abundant representative of the entomofauna of oak stands in the Czech Republic. In 2014, its biology was studied at ten sites in the Brno region. During the growing period, 35 inspections were made in the studied stands at intervals from three to seven days. Main results obtained through field and laboratory studies are as follows:

1. Leaf rolls were found on *Quercus* spp. and sporadically on *Castanea sativa*. Host oak species were *Q. petraea* (66 %), *Q. dalechampii* (22 %), *Q. robur* (7 %), *Q. pubescens* (2.5 %) and *Q. cerris* (2.5 %). The leaf rolls were not observed on any other tree species. The pest colonizes trees of the first age class, rarely lower branches of older trees.

2. Hibernating in the leaf rolls of which 80 % are fallen onto the ground are grown-up larvae of the 2nd instar. These pupate in the rolls from the second half of April to the beginning of May.

3. Beetles fly onto the host trees usually at the end of April and beginning of May. The population is slightly dominated by females (sexual index being 0.55). Males are more abundant at the beginning of the eclosion period, which lasts 3–4 weeks (sex ratio 2:1), females are more abundant towards the end of the period (0.7:1). The beetles are 3.3–6.3 (on average 5.2) mm long. No differences were observed between the size of males and females. The average size of beetles decreases during the eclosion period.

4. The beetles bite out linear feeding notches into the leaf blade from the adaxial face that are on average 4.7 mm long and 1.3 mm wide, windowing the leaves (90 %) and skeletonising them (10 %). Veins and vein anastomoses remain intact. The beetles live on average two months and damage ca. 30 cm^2 of reduced leaf area.

5. Sexually mature fertilized females seek for rolling freshly budded leaves of a certain size, shape and consistence. At first, the female bites out a mine into the main vein of the selected leaf, reaching as far as to the lower epidermis. She makes a puncture in the vein at 1/3 of its length (ca. 3 mm from the contact point of subsequent cross cuts with the vein), i.e. in the basal (unrolled) part of the blade. Then she bites out two 1 mm wide cross cuts at a third of the blade length, running from blade margins up to the main vein where the cuts meet at one point. She bites out 150–622 (on average 348) cross cuts into the leaf veins, which facilitate their bending. The most obvious and numerous (even twin at the vein base) are cuts on the abaxial face of the main vein.

6. At first, the female folds the flexible wilting part of the blade adaxially along the main vein. Then she lays 1–5 (on average 1.1) eggs into the blade tip fold (up to 15 mm from the apex) and rolls the folded leaf from the tip into a neat cylindrical roll, which is on average 8.9 mm long and 6.6 mm wide. Eggs are on average 0.83 mm long and 0.68 mm wide. The female usually creates 3.2 (3.8) leaf rolls on the primary (secondary) shoots. Within 1.5–2.5 months, she usually creates 23 leaf rolls and lays ca. 25 eggs.

7. In three weeks, larvae of the 1st instar emerge from the eggs, which damage 0.2–0.3 cm^2 of leaf area within 2–5 weeks. In July and in the first half of August, the larvae grow up to the length of 2.2–3.2 mm and width of 0.9–1.2 mm. Their cranium is 0.43–0.54 mm wide. Larvae of the 2nd instar continue in eating out the leaf roll inside and at the end of the growing season their length is 4–6.4 mm and width 1.7–2.5 mm. They damage 1.5–2.0 cm^2 of leaves. Their cranium is 0.7–0.8 mm wide.

8. In the spring, the females create rolls on the leaves of primary shoots. The average area of intact (damaged) leaves on these shoots was 18.0 cm^2, (13.8 cm^2 – i.e. by 23.3 % smaller). Secondary shoots develop on the most vital primary shoots of oaks in the second half of June. The average area of intact (damaged) leaves on the secondary shoots was 14.6 cm^2 (15.0 cm^2 – i.e. by 2.7 % larger). This indicates that on the primary shoots (with relatively large leaves), the females chose leaves of below-average size for rolling. On the secondary shoots (with relatively small leaves), however they roll rather average- to above-average sized leaves. With the increasing length of shoots, the percentage of rolled leaves decreases and the area of intact and damaged leaves increases.

9. Of the total average area of damaged leaves (14.3 cm^2), 2.4 cm^2 (16.8 %) went to the unrolled base while 11.9 cm^2 (83.2 %) went to the rolled part of the leaf blade. More than 75 % of rolls fell from trees before winter.

10. A factor very important for *A. nitens* mortality is very warm and dry weather. Due to extreme weather in May and June 2014, some 20 % of eggs and 1st instar larvae died in the Brno region. Imagos of *Poropoea stollwerckii* Först. (Trichogrammatidae) emerged from 1.6 % of eggs. Imagos of Braconidae family emerged from 1.8 % of leaf rolls and Ichneumonidae imagos emerged from 0.1 % of leaf rolls. Larvae of Tachinidae killed about 40 % of beetles in June. *Lasiorhynchites sericeus* (Hbst.) (Rhynchitidae), often mentioned in the literature, was not observed in the leaf rolls in the Brno region. In the Vranov forest district, 75 % of rolls on the leaves of coppice shoots were grazed off by *Capreolus capreolus* (L.). Leaf rolls persisting on trees were pecked out by birds in the period of vegetative quiet. During the growing season, 36 % of individuals (15 % of eggs, 16 % of 1st instar larvae and 5 % of 2nd instar larvae)

died in leaf rolls on the primary shoots while 28 % of individuals (22 % of eggs, 5 % of 1st instar larvae and 1 % of 2nd instar larvae) died in leaf rolls on the secondary shoots.

11. *A. nitens* never does harm to shoots themselves. Its harmfulness is relatively low and therefore its control is usually not necessary.

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