JOURNAL OF FOREST SCIENCE, *52*, 2006 (8): 357–385

Occurrence, development and economic importance of *Phratora* (= *Phyllodecta*) *vitellinae* (L.) (Coleoptera, Chrysomelidae)

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ABSTRACT: The paper summarizes results of the study of the occurrence, development and harmfulness of *Phratora* (= *Phyllodecta*) *vitellinae* (L.). The majority of studies was carried out in 1998 to 2005 in riparian and accompanying stands of the Svitava and Svratka rivers in the region of Brno and in a laboratory. Imagoes leave hibernation hiding places at the end of April and at the beginning of May. In captivity, they lived on *Salix fragilis* about 2.5 months damaging on average 28.6 cm^2 leaf blades and laying on average 293 eggs. In the excessively warm growing season of 2005, imagoes lived about 3.5 months after hibernation, however, already after one month of feeding they fell in a month diapause at the beginning of June. Before its start, they damaged on average 12.8 cm^2 (after the diapause 14.4 cm^2) leaves and laid on average 389 eggs (of this number, 260 eggs before and 129 after the diapause). Larvae damage about 4 cm^2 leaves during 2 to 3 weeks (in the laboratory during 12 to 13 days). After 2 to 3 weeks (in the laboratory after 10 to 12 days) from the cessation of feeding young beetles appear on trees. Imagoes of the 1st generation occur from mid-June to the beginning of October. During about 55 days of life, they damaged 19 cm^2 leaves and laid on average 182 eggs. Imagoes of the 2nd generation occur from mid-August to the end of the growing season. After 10 to 14 days of feeding (without previous copulation), they take shelter in wintering places. In the laboratory, however, these imagoes damaged about 19 cm^2 leaves during 2 months and laid about 190 eggs. Wintering places were looked up by imagoes of the 3rd generation which damaged on average 4.2 cm^2 leaves before hibernation. In the Czech Republic, *P. vitellinae* is usually bivoltine the 2nd generation being always incomplete.

Keywords: Chrysomelidae; *Phratora* (= *Phyllodecta*) *vitellinae*; occurrence; host species; development; generation conditions; harmfulness

In the region of the CR, 5 species of chrysomelids of the genus *Phratora* Chevr. (= *Phyllodecta* Kirby) occur. Members of the genus create morphologically, biologically and ecologically a uniform group which is distributed mainly in the northern temperate zone. Their phylogenesis broadly coincides with the species spectrum and chemical composition of host species. As for nutrition, particular chrysomelids specialized in various degree to species of the family Salicaceae. *P. vittellinae* (L.) ranks among the most abundant and forestry-most important domestic members of the genus and of the whole family of Chrysomelidae. This chrysomelid occurs on many species of willows (*Salix* spp.) and poplars (*Populus* spp.). Under favourable conditions, it reproduces often on a mass scale and then heavily damages particularly young trees. Temperate and dry winters and excessively dry and warm springs participate in its activation. In the CR, population densities of *P. vitellinae* and a number of other phyllophagous species of chrysomelids generally increased in obvious connection with climatic-meteorological anomalies and the primary physiological weakening of trees during last decades. The occurrence, biology and harmful-

Supported by the Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry Brno within the Research Plan MSM No. 6215648902.

ness of some forestry-important chrysomelid species which gradated in Moravia recently were studied by Urban (1997, 1998a,b, 1999, 2000, 2005, 2006, etc.). This paper deals with findings obtained through field and laboratory studies of *P. vitellinae*.

P. vitellinae occurs in the best part of Palaearctic and Nearctic zoogeographic regions. Thus, in principle, it is a Holarctic (according to Warchalowski 1973 Eurosiberian) species its centre of distribution being the Eurosiberian subregion. Already Calwer (1876) mentioned its occurrence in Germany, Hungary, Illyria (i.e. in the part of the present Croatia and Slovenia), Italy, France, England and Sweden. According to Escherich (1923), the area of its occurrence extends from France up to the mouth of the Amur river and from the Caucasus up to Lapland and in North America. Hellén et al. (1939) rank it among broadly distributed Fennoscandinavian species (including Karelia and Lapland). According to the author, it is even more distributed there than a sympatric species *P. vulgatissima* (L.). It is also considered to be a very abundant Holarctic species with similar economic importance as *P. vitellinae*. Considering rather similar ecological requirements both species occur often in the same localities and even on the same species. Arnoldi et al. (1955) complete the natural range of *P. vitellinae* mentioning it in Algeria, whole Europe and the Caucasus (with the exception of the steppe zone of the European part of the former USSR), Siberia, the seabord of Far East and North America. Similarly, the geographical occurrence of *P. vitellinae* is mentioned by Vasiljev et al. (1974). According to the authors, the chrysomelid was also found in Kamchatka and the Kurile Islands. Its vertical distribution reaches from lowlands up to high locations above the forest limit (Maisner 1974).

P. vitellinae together with *P. vulgatissima* and *Plagiodera versicolora* (Laich.) belong to the most abundant and most harmful mainly blue or green coloured chrysomelids on tree species from the family Salicaceae. Various aggregate publications and specialized entomological and entomological-forest protection papers deal with its occurrence, development, harmfulness and possibilities of protection. During last three decades, about 150 scientific papers on *P. vitellinae* were published in Europe (particularly in Belgium, Great Britain, Germany, Finland and Sweden). The greatest attention was paid to its feeding selection, i.e. the effect of physical properties and chemical composition of leaves of host species on the occurrence, fecundity, rate of development and mortality.

According to Ratzeburg (1839), *P. vitellinae* often damages leaves of willows. According to Kaltenbach (1874), it occurs abundantly on smooth-leaf willows and *Populus nigra* L. For example, Henschel (1876) and Kuhnt (1913) rate the beetle among generally leaf-eating species on willows while Calwer (1876) rate it among leaf-eating species on *P. tremula* L. A number of authors (Reitter 1912; Fleischer 1927–1930; Rubner et al. 1942; Javorek 1947; Medvedev, Šapiro 1965; Mohr 1966; Warchalowski 1973; Maisner 1974; Vasiljev et al. 1975) limits itself to the general statement of the beetle occurrence on willows and poplars. However, e.g., Nüsslin and Rhumbler (1922) mention that *P. vitellinae* attacks in preference *S. purpurea* L. and allegedly also *S. caprea* L. and poplars. *S. triandra* L. is considered to be resistant (however, in case of lack it damages reputedly its hybrids). Also Escherich (1923) mentions that not all species of willows are attacked. He regards *S. purpurea*, *S. viminalis* L. and *S. caprea* as very favourite and *S. triandra* as quite neglected. In Austria, Pernersdorfer (1941) found *P. vitellinae* on *S. fragilis* L., *S. purpurea* and *P. tremula*. However, she observed intense feeding only on *S. fragilis*. Except *S. purpurea* also *S. alba* L. var. *vitellina* (= *S. vitellina* L.) (Blunck et al. 1954) are main host plants. According to Arnoldi et al. (1955) it occurs not only on *S. purpurea*, *S. viminalis* and poplars but also on *Alnus hirsuta* (Spach.) Rupr. Vasiljev et al. (1974) rank *S. purpurea*, *S. viminalis*, *P. nigra* L., *P. nigra* L. var. *italica* and sometimes also *Alnus* sp. among its most searched hosts. The chrysomelid is sporadically reported from *Betula* sp. (Schaufuss 1916; Roubal 1937–1941). It was obviously related to accidental finds of imagoes of a wintering generation during their posthibernation migrations.

P. vitellinae is known particularly as the pest of willows in osier plantations, i.e. in willow stands with a 1(2)-year rotation intended for the production of wicker for basketry (Escherich 1923; Rubner et al. 1942; Schwerdtfeger 1944; Živojinovič 1948; Nejedlý 1950; Blunck et al. 1954; Gäbler 1955; Schnaider 1957; Wagner, Ortmann 1959; Kadłubowski, Czalej 1962; Urban 1982, etc.). Recently, it becomes to occur as the pest of willows and poplars in "energy plantations". Young intensively growing trees create also optimum conditions for the gradation of many other pest herbivores. *P. vitellinae* frequently heavily damages plantations of *S.* cv. *Americana* imported to Europe (Wagner, Ortmann 1959; Kadłubowski, Czalej 1962, etc.). Also Czerniakowski (2002) found its dominant proportion (within the genus *Phratora*) in a plantation of *S.* cv. *Americana.* In agreement with Köpf et al. (1998) the author assumes that it refers to a species with rather broad trophic plasticity.

Goidanich (1983) mentions damage to willows particularly at medium and higher altitudes of Italy. According to Rowell-Rahier and Pasteels (1982), *P. vitellinae* occurs mainly on *S. nigricans* Sm. (= *S. myrsinifolia* Sal.) the leaves of which contain phenolic glucosides (mainly salicin) and usually do not occur on the abaxial face densely covered with trichomes. The author ranks *S. cinerea* L. and *S. caprea* among neglected species not containing these secondary metabolites, however, their leaves are densely covered with trichomes on the abaxial face.

Larvae of *P. vitellinae* excrete in danger a defensive secretion from 2 pairs of thoracic and 7 pairs of abdominal dorsal glands containing salicylaldehyde which is derived from salicin in leaves of host species (Soetens 1997; Pasteels et al. 1983, 1988, 1990; Brückmann et al. 2002, etc.). The larval secretion is considered to be a defensive substance against nonspecific predators and parasitoids. Hilker (1989) demonstrated that the secretion of a chrysomelid operated as a repelent even on conspecific imagoes and imagoes of other competitive phyllophagous species of chrysomelids (e.g., as against *Plagiodera versicolora*). Active social behaviour of larvae of *P. vitellinae* is an ecological adaptation to physical and chemical properties of host species and to the protection from some natural enemies and unfavourable weather (Grégoire 1988). The gregariousness increases the defence of particular larvae both through the cumulative effect of toxins and due to conspicuity and colour polymorphism of groups of larvae created by the fancy mixture of white and black individuals. The gregariousness also increases rather limited potential of egg larvae to bite their way out through the intact leaf epidermis. A mutual contact and tigmotaxis stimulate the feeding of larvae inhibiting their movement (Grégoire 1988). The secretion increases the immunity system of larvae showing antibacterial and fungicidal effects (Gross et al. 2004). Unlike larvae imagoes of *P. vitellinae* synthesize their own defensive substances incorporating them into eggs. However, the absence of salicin as the precursor of salicylaldehyde is not decisive for food intake. It is, for example, demonstrated by laboratory experiments of Rowell-Rahier and Pasteels (1982) where larvae willingly consumed leaves of *S. caprea* deprived of trichomes, however, did not excrete secretions containing salicylaldehyde. The secretion of salicylaldehyde was restored after the addition of salicin to leaves. Rowell-Rahier (1984a) mentions *P. vitellinae* mainly on *S. nigricans* and *S. hegetschweileri* Heer, less frequently on *S. purpurea*, *P. tremula* and *P. trichocarpa* Torr et Gray × *P. deltoides* Marsh. Defoliation obviously does not induce the resistance of *S. nigricans* to *P. vitellinae*. Rowell-Rahier (1984b) found (in the laboratory) the following order of host plants according to the decreasing trophic preference: *S. nigricans*, *S. purpurea*, *P. nigra*, *P. tremula*, *S. alba*, *S. caprea* and *S. cinerea*. Leaves of *S. nigricans* are richest in salicin and leaves of three least consumed willows are densely pilose on the abaxial face. In populations of *P. vitellinae* obtained from geographically different localities in Central Europe, there are certain dietary specializations which can be induced by laboratory conditions.

The resistance of some poplar clones to *P. vitellinae* was studied by Finet and Gregoire (1981, 1982), Finet et al. (1982, 1983) in a glasshouse, nature and laboratory. The authors proved the very high resistance of a clone *P. nigra* Ghoy 1 and the considerable resistance of a clone *P. trichocarpa* Fritzy Pauly. On the other hand, clones *P. trichocarpa* × *deltoides* Unal and Beaupré were very disposed. According to Finet and Gregoire (1981) imagoes are equally active at night as during the day most active being at dusk.

Trophic relationships between *P. vitellinae* and the spectrum and concentration of phenolic glucosides of 4 autochthonous and 4 introduced species of willows were studied by Tahvanainen et al. (1985) in Finland. The chrysomelid preferred a native smooth-leaved *S. nigricans* the leaves of which contained extraordinary high concentrations of phenolic glucosides (mainly salicortine and salicin). It consumed intensively medium-densely pilose leaves of imported *S.* cv. *Aquatica* and *S. dasyclados* Wimm. with the medium concentration of glucosides. *P. vitellinae* refused to consume smooth leaves of *S. triandra* which contain the medium concentration of glucosides but a different dominant glucoside salidrosid. Also *S. pentandra* L. the glabrous leaves of which contain considerable amounts of mostly little known or unknown glucosides was rather resistant. Sericeous pilose leaves of *S. viminalis* and glabrous leaves of *S. phylicifolia* L. show the low general concentration of phenolic glucosides. The trophic affinity of imagoes and larvae to *S. phylicifolia* is evidentially lower than that to *S. pentandra* (Rank et al. 1998). *S. fragilis* is characterized by the high concentration of usual glucosides and glabrous leaves. Therefore, *S. fragilis* is far more damaged than *S. alba* the leaves of which are densely pilose being characterized by the low concentration of phenolic glucosides (Soetens, Pasteels 1988; Soetens et al. 1991). During oviposition, females of *P. vitellinae* highly preferred *S. fragilis* to *S. viminalis* and *S. dasyclados* (Denno et al. 1990). Nevertheless, larvae developed well on leaves of

S. viminalis which were poor in salicylates. Considering the absence of a defensive secretion these larvae are, however, vulnerable towards general predators. Effects of phenolic glucosides on the trophic behaviour of *P. vitellinae* were also demonstrated by Kolehmainen et al. (1995), etc.

Hallgren (2003) and Hallgren et al. (2003) dealt with the effect of the hybridization of *S. caprea* and *S. repens* L. on the concentration of secondary compounds in leaves and on insect herbivores (including *P. vitellinae*). Interactions between *P. vitellinae* and a primary host plant *S. nigricans* (or secondary host plant *S. phylicifolia*) and *P. vitellinae* in the environment with elevated UV radiation were studied by Veteli et al. (2002). An increase in UV-B radiation did not affect any measurable characters of the food quality. However, the abundance of imagoes on treated trees was higher than on control trees. While the growth of larvae was not affected by UV radiation on treated trees of *S. nigricans*, on *S. phylicifolia* was retarded. Thus, the authors assume that specialized herbivores (i.e. also *P. vitellinae*) can be more sensitive to secondary changes in secondary hosts than in primary hosts. Veteli et al. (2002) dealt with the study of the effect of increased temperature and CO_2 concentration on the metabolism of *S. nigricans* and feeding of imagoes (including the growth of larvae) of *P. vitellinae.* With the increase of both climatic elements the above-ground biomass increased and the total concentration of phenolic substances in leaves decreased. With the increased CO_2 concentration the content of water and N in leaves decreased. With the increased CO_2 concentration the consumption of food and the period of life of imagoes can increase and the relative rate of the growth of larvae decrease (unlike temperature accelerating the growth of larvae).

Some other problems of the biology of *P. vitellinae* including its life cycle, natural enemies, harmfulness and control were also studied. For example, egg laying and their embryonal development were studied by Zachvatkin (1967). Temperature requirements of some chrysomelids (including *P. vitellinae*) were determined by Kadłubowski and Dudik (1968). Kendall and Wiltshire (1998) mentioned the life cycle of *P. vitellinae* in a plantation of *S. viminalis*. Sage et al. (1999) described the posthibernation migration from wintering habitats to poplar plantations and the secondary colonization of plantations. According to Peacock et al. (2003) ecological niches of *P. vitellinae* and *P. vulgatissima* are considerably different due to differences in the food preference. However, both species occur sometimes together and on the same tree species (in Great Britain, e.g. on *S. burjatica* Nas. Germany and in early spring on *P. trichocarpa* Torr et Gray Trichobel) and sometimes even mate with one another. However, the reproduction isolation of both species is perfect because larvae hatch from laid eggs sporadically and always die during a week (Peacock et al. 2004).

An unexpected ecological role of the secretion of *P. vitellinae* larvae in the trophic behaviour of a hover fly *Parasyrphus nigritarsis* (Zett.) (Syrphidae) was demonstrated by Köpf et al. (1997). Larvae of this specialized predator are surprisingly attracted both by the secretion of larvae of the chrysomelid and by pure salicylaldehyde (i.e. the main component of the secretion). Thus, the hover fly uses the chrysomelid secretion to localize its prey. For general predators, such as predaceous ants salicylaldehyde in the chrysomelid secretion is an effective repellent (Pasteels et al. 1983). Thus, larvae of *P. vitellinae* on *S. nigricans* are killed by predaceous ants less than general leaf-eating herbivores on *S. phylicifolia* (Sipura 2002). According to Palokangas and Neuvonen (1992) *P. vitellinae* is attacked by spiders much less on *P. tremula* and *S. nigricans* than *P. polaris* Schn. on *Betula pubescens* Ehrh. (free of glucosides). Receptivity of 5 species of imagoes (including *P. vitellinae*) to *Phylloscopus trochilus* L. (Aves) was tested by Lundvall et al. (1998) in an aviary. In species with the different type of chemical defence feeding on *Salix*, birds destroyed somewhat more *Galerucella lineola* (F.) than *P. vitellinae* and *Gonioctena viminalis* (L.). In another experiment with chrysomelids of the same type of defence birds preferred *Phratora polaris* Schn. (from *Betula* sp.) to *P. vitellinae* (from *Salix* sp.). They looked for least *Chrysomela lapponica* L. (with a marked aposematic colour).

P. vitellinae is an economically important pest of young willows and poplars (Tuinzing 1946; Györfi 1952; Charvát, Čapek 1954; Timčenko, Treml 1963; Kasap 1988; Sage, Tucker 1997; Glavas et al. 1997; Gruppe et al. 1999; Aslan, Ozbek 1999; Jaskiewicz et al. 2004, etc.). Recently, problems of the effective control of the pest were, e.g. dealt with by Attard (1979), Jodal (1985), Allegro (1989), Moraal (1989) and Karp (2003).

MATERIAL AND METHODS

The majority of field and laboratory studies was carried out in 1998 to 2005. In nature, the chrysomelid was studied mainly in riparian and accompanying stands of the Svitava and Svratka rivers in the region of Brno. The investigated stands are situated at an altitude of 190 to 230 m. Mean annual temperatures are 8.4°C and mean annual precipitation 547 mm. In the mixture of species of various age the family of Salicaceae was represented, e.g. by *S. fragilis*, *S.* × *rubens* Schr., *S. alba*, *S. triandra*, *S. purpurea*, S. × *rubra* Huds., *S. viminalis*, *P. nigra*, *P. nigra* var. *italica*, *P. alba*, *P. tremula*, *P.* × *canescens* (Ait.) Sm., etc. Field inspections were carried out throughout the growing season, namely usually in 2-week intervals. Occasionally, trees were also checked in forest stands of the Křtiny Training Forest Enterprise and of the Židlochovice Forest Enterprise. In 1969 to 1975, integrated research was carried out into insect pests in 6 osier plantations (with 12 cultivated clones of willows) in Moravia. Urban (1982) briefly reported on the occurrence, bionomy and harmfulness of *P. vitellinae*.

Findings from nature were compared with results of extensive laboratory rearings on *S. fragilis* and tentatively also on some other species of Salicaceae. For the rearings, glass vessels of a diameter of 10 (20) cm and height 5 (10) cm were used. Into the vessels, fresh leaves (more sporadically 5 to 15 cm long filiaged sections of 1-year-old shoots) were put in regular 2-day intervals (in rearings of larvae in 1-day intervals). These were always taken from the same tree and from the same part of a crown. Leaf petioles (or lower ends of shoot sections) were wrapped by a bit of moistened cotton wool. Less frequently, they were put into small vessels with water necks of the vessels being sealed by cotton wool.

In individual and mass laboratory rearings of imagoes carried out throughout the growing season the damaged area of leaves was regularly determined every second day using planimetry. The number of laid eggs (including the number of eggs destroyed by imagoes) and the number and localization of egg groups on a leaf blade were recorded. The length was measured of male and female bodies and in dead females, the number was determined of unlaid eggs using the microscopic dissection of ovaries. In 2005, the number of frass pellets and their dimensions were recorded. During long-term rearings, findings were obtained on the life of imagoes of particular generations and the course of feeding and egg laying.

Attention was paid to the preimaginal (particularly larval) development of *P. vitellinae*. Larvae were reared on leaves of *S. fragilis* (or other species of Salicaceae), viz 1 to 30 pieces from May to October. Every day, the size was recorded of the instar of larvae as well as mortality and damaged leaf area. Instars were determined by means of micrometry according to the width of cranium. In 2005, the number and dimensions of frass pellets of larvae of particular instars were recorded daily. Earth for pupation was put in the bottom of vessels for growing up larvae. In case of the small volume of earth it was possible to observe pupation and maturation of newly hatched imagoes through glass walls of vessels in pupal chambers.

RESULTS AND DISCUSSION

Host species

Tahvanainen et al. (1985), Soetens et al. (1991), Kolehmainen et al. (1995), etc. note that chemical and physical characteristics of leaves of host species are a good indicator of the abundance of insect herbivores. Unlike *P. vulgatissima* and *Galerucella lineola* a chrysomelid *P. vitellinae* occurs most frequently on species with smooth leaves on the abaxial face and with leaves medium-rich and rich in phenolic glucosides. The feeding selection is in correlation with the content and species spectrum of these compounds. The absence or lack of secondary substances in the food of *P. vitellinae* (e.g. in leaves of *S. viminalis* and *S. caprea*) is not critical for food intake being, however, decisive for the defensive secretion of larvae. Relation to glucosides manifests in the trophic specialization which evidently did not reach such a degree as in other members of the genus *Phratora*.

In osier plantations in Moravia, *P. vitellinae* was found most frequently on *S. purpurea*, *S.* × *rubens* and frequently on *S. viminalis* and *S.* × *rubra* and *S.* cv. *Americana*. In riparian and accompanying stands of the Svitava and Svratka rivers in the Brno region, the chrysomelid occurred most frequently on *S. fragilis*, *S. purpurea* and *S.* × *rubens*, less frequently on *S. viminalis* and *P. tremula*. It was not found on *S. triandra*, *S. caprea*, *S. alba*, *P. nigra* and *P.* × *canescens*. Neglected species are characterized either by the considerable concentration of unusual glucosides in leaves perhaps even by their small amount or absence or densely pilose abaxial face of the leaf blade.

Findings from nature generally agree with results of laboratory tests. In addition to the above mentioned primary host species imagoes consumed, in case of the lack of more suitable food, also *S. caprea*, *S. alba* and *S. acutifolia* but always refused *S. triandra*. If imagoes had the possibility of selection they always willingly consumed *S. fragilis*, *S. purpurea* and *S.* × *rubens* and refused *S. viminalis*, *S. caprea*, *S. alba*, *P. nigra*, *P. nigra* var. *italica* and *P. alba*. In the laboratory (i.e. under conditions of the absence of natural enemies), larvae developed quite normally on *S. viminalis* and *S. caprea*. For example, larvae of the 1st generation fed on *S. viminalis* on average

12 days. Within the time, they damaged on average 2.7 cm² leaves and produced on average 400 frass pellets. On *S. caprea*, larvae of the same generation fed on average 14 days damaging on average 3.0 cm² leaves and defecated on average 300 frass pellets. On a trophically optimum host species *S. fragilis,* larvae developed on average 12 days, damaged on average 2.9 cm² leaves and defecated on average 600 frass pellets.

There are many factual data concerning the disposal of trees to *P. vitellinae* damage some of them differing diametrically from each other. Therefore, determination of the objective order of species according to the degree of resistance is not yet possible. In a simplified fashion it is possible to state that *S. fragilis*, *S. nigricans* and *S.* × *rubens* rank among the most favourite domestic species. In our country, *S. purpurea* and obviously also *P. tremula* are damaged very frequently. Nevertheless, Rowell-Rahier (1984a) assumes that *S. purpurea* is not suitable for egg laying and the development of larvae. *S. viminalis*, *S.* × *rubra* and *S.* cv. *Americana* are often damaged. Evidently only rarely or even sporadically (e.g. in insect outbreak on primary hosts), the pest occurs on *S. caprea*, *S. alba*, *S. alba* var. *vitellina* and *S. cinerea.* For example, *S. triandra*, *P. alba*, some clones of *P. nigra* etc. are quite resistant.

Hibernation of beetles and leaving winter habitats

According to Nüsslin and Rhumbler (1922) imagoes of *P. vitellinae* winter in the ground, in bark fissures, between buds in whorls of pines and in hollow plant stems. Localization of hibernation places was specified by Escherich (1923). According to the author imagoes winter mostly on protected elevated places, viz e.g. between non-fallen twisted leaves, between terminal buds of pines, in hollow stems of plants, under loosened bark of trees and in corridors of bark beetles. For example Wagner and Ortmann (1959) mention the most frequent wintering under bark, in dry leaves on trees, in fissures of fences and stubs of sticks or in soil between fallen leaves.

According to Schnaider (1972), in autumn imagoes fly from osier plantations to neighbouring forests and shrubs where they winter in fissures of bark, in litter etc. Kendall and Wiltshire (1998) found imagoes in cancerous tumours on willows in plantations and in fissures of wooden posts and in cardboard hibernation traps in the surroundings up to 100 m from a plantation. Also a related *P. vulgatissima* was found by the authors mostly in the close vicinity of plantations (within 100 m) while part of

Table 1. Average week area of leaves of *S. fragilis* damaged by imagoes of *P. vitellinae* after wintering. Imagoes were caught at the beginning of the period of feeding in Bílovice nad Svitavou (in 1999* in Adamov and in 2001 in Žďár nad Sázavou). Laboratory rearings on *S. fragilis*

Week	Period	1998		1999		1999*		2001	
		(cm²)	(%)	(cm²)	(%)	(cm²)	(%)	(cm²)	(%)
1st	4–10 May	2.4	12.5	2.4	10.8	2.5	7.3	–	–
2nd	11–17 May	3.0	15.6	3.1	13.9	3.1	9.1	?	?
3rd	18–24 May	4.2	21.9	2.8	12.6	3.4	9.9	1.9	5.3
4th	25–31 May	2.7	14.1	2.8	12.6	3.5	10.2	3.6	10.0
5th	1–7 June	2.5	13.0	2.8	12.5	4.0	11.7	2.6	7.2
6th	8–14 June	2.1	10.9	2.5	11.2	4.0	11.7	1.7	4.7
7th	15–21 June	1.4	7.3	2.3	10.3	4.4	12.9	4.4	12.2
8th	22–28 June	0.7	3.6	1.3	5.8	3.4	9.9	2.9	8.0
9th	29–5 July	0.2	1.1	1.3	5.8	2.3	6.7	4.0	11.1
10th	6–12 July	–	–	0.6	2.7	1.5	4.4	4.6	12.7
11th	13–19 July	–	–	0.4	1.8	1.0	2.9	4.1	11.4
12th	20–26 July	–	–	0	0	0.6	1.8	2.6	7.2
13th	27–2 August	–	–	–	–	0.4	1.2	2.4	6.6
14th	3–9 August	–	–	–	–	0.1	0.3	1.3	3.6
15th	10–16 August	–	–	–	–	–	–	0	0
Total		19.2	100.0	22.3	100.0	34.2	100.0	(36.1)	100.0
Number of ♂♂/♀♀		8/8	–	10/6	–	4/6	–	3/4	–

Fig. 1. Imagoes of *Phratora vitellinae* during feeding on the abaxial face of leaves of *Salix fragilis*. Laboratory rearing, 18 May 1998

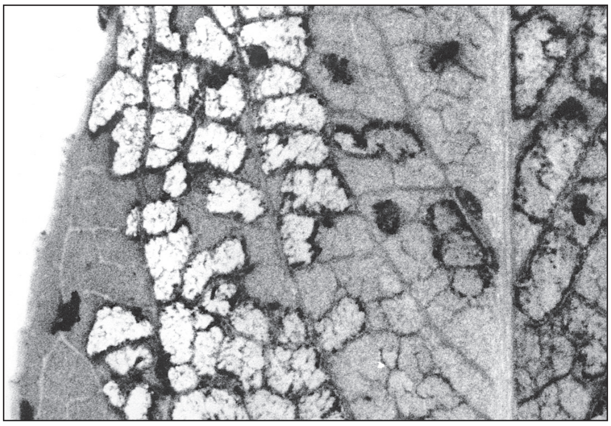

Fig. 2. A detail of damage to the abaxial face of leaves of *S. fragilis* by imagoes of *P. vitellinae*. Bílovice nad Svitavou, 15 May 1998

imagoes hibernated in plantations (e.g. in fissures of willow stems, in dead vegetation and in litter). It is possible to suppose that with the increasing distance of suitable hibernation shelters imagoes will show higher tendency for hibernation in plantations (Kendall, Wiltshire 1998). Sage et al. (1999) mention the considerable flying activity of imagoes of a wintering generation. The authors found that majority of imagoes wintered under the bark of full-grown coniferous and broadleaved trees at a distance up to 250 m from plantations. According to the authors imagoes winter in shelters either individually or in variously numerous close aggregations (up to 500 beetles).

With the increasing length of a "light day" and growth of spring temperatures beetles of the wintering generation become active. Usually at the end of April (Achremowicz 1960) (under conditions of colder weather already at the beginning of May – Kadłubowski, Czalej 1962), they occur on host species. According to Escherich (1923), Živojinovič (1948), Nejedlý (1950), Schnaider (1972), etc. beetles occur after hibernation usually in April, according to Maisner (1974) sporadically already in March. According to Sage et al. (1999) they fly mainly on the border 8-meter-wide zone of plantations where about 80% beetles are accumulated. During next about 3 weeks, the beetles gradually spread in a stand (secondary dispersion). In the region of southern Moravia, beetles leave wintering shelters usually at the end of April; in the region of central Moravia usually at the end of April and at the beginning of May.

Beetle feeding after wintering

After the very long (about 8 months) period of hibernation, beetles are extremely starved and weakened. Therefore, as soon as the chrysomelids reach host species they begin to damage unfolding (or newly flushed) leaves. In case of the retarded start of budbreak they damage buds and fine bark at the end of young shoots. They eat petty irregular holes into the blade of leaves from the abaxial face

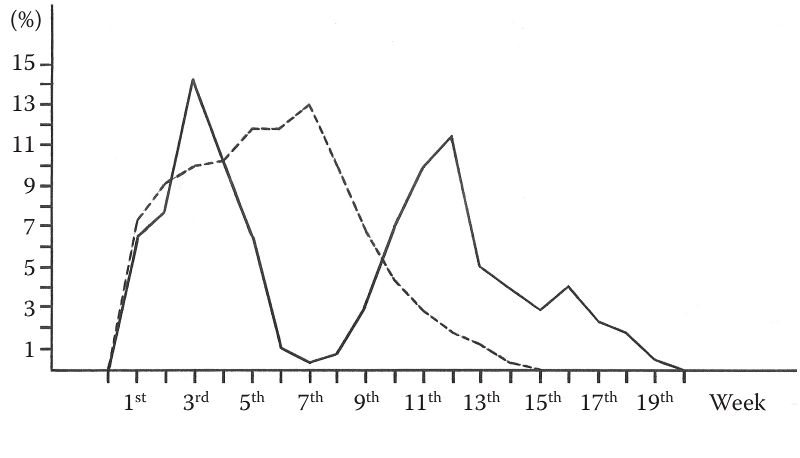

Fig. 3. The course of damage to leaves of *S. fragilis* by imagoes of *P. vitellinae* after their hibernation in nature (in % of the total damaged area). Laboratory rearings, 1999 (dash line), 2005 (solid line)

Table 2. Average week area of leaves of *S. fragilis* damaged by imagoes of *P. vitellinae* after wintering. Imagoes were caught at the beginning of the period of feeding on *S. fragilis* in Bílovice nad Svitavou. Laboratory rearings on *S. fragilis*, 2005

Week	Period	Rearing 1		Rearing 2		Rearing 3		Rearing 4		Rearing 5	
		(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)
1st	4–10 May	2.8	9.1	2.6	11.3	1.5	4.0	1.3	4.0	0.8	6.1
2nd	11–17 May	2.9	9.4	2.7	11.7	1.9	5.3	1.6	5.0	1.3	10.0
3rd	18–24 May	5.0	16.2	5.0	21.6	4.3	11.7	3.2	9.9	1.7	13.1
4th	25–31 May	3.0	9.8	4.3	18.6	3.1	8.4	2.3	7.1	1.4	10.8
5th	1–7 June	3.0	9.8	1.7	7.4	3.2	8.7	0	0	1.1	8.5
6th	8–14 June	0.4	1.3	0	0	0.1	0.3	0	0	0.9	6.9
7th	15–21 June	0.2	0.6	0	0	0	0	0.1	0.3	0.4	3.1
8th	22–28 June	0.8	2.6	0	0	0	0	0.1	0.3	0.2	1.5
9th	2–5 July	2.1	6.8	0	0	0	0	1.6	5.0	0.2	1.5
10th	6–12 July	2.4	7.8	0.8	3.5	2.2	5.9	3.2	9.9	1.5	11.5
11th	13–19 July	4.0	13.0	1.4	6.1	2.7	7.3	4.0	12.4	1.6	12.3
12th	20–26 July	3.4	11.0	1.5	6.5	4.5	12.2	4.8	14.9	1.1	8.5
13th	27–2 August	0.8	2.6	0.7	3.0	3.0	8.1	1.8	5.6	0.8	6.2
14th	3–9 August	0	0	0.7	3.0	3.6	9.8	1.4	4.4	0	0
15th	10–16 August	–	–	0.5	2.2	2.0	5.4	1.4	4.4	–	–
16th	17–23 August	–	–	0.4	1.7	3.2	8.7	2.0	6.2	–	–
17th	24–30 August	–	–	0.4	1.7	1.0	2.7	1.4	4.4	–	–
18th	31–6 September	–	–	0.4	1.7	0.5	1.4	1.7	5.3	–	–
19th	7–13 September	–	–	–	–	–	–	0.3	0.9	–	–
20th	14–15 September	–	–	–	–	–	–	0	0	–	–
Total		30.8	100.0	23.1	100.0	36.8	100.0	32.2	100.0	13.0	100.0
Number of ♂♂/♀♀		1/1	–	1/1	–	1/1	–	0/2	–	2/0	–

(in the laboratory, some 20% of the blade area also from the adaxial face). Budding leaves are always perforated by the beetles; newly unfolded leaves are partly perforated and partly skeletonized. Older leaves are always skeletonized, all venation of leaves and upper epidermis being left intact (Figs. 1 and 2). Beetles damage mostly semi-developed or newly unfolded leaves. Little flushed or old leaves are mostly neglected. Particularly old leaves are nutritionally the very poor source of food for beetles and their reproduction (Raupp, Sadof 1991). Holes in little developed leaf blades are on average about 4 mm long and 3 mm wide. Holes in full-grown blades are on average 0.9 mm long and 0.6 mm wide.

Imagoes of the wintering generation caught in 1998 to 2001 at the beginning of the period of feeding lived in laboratory rearings on *S. fragilis* 1.5 to 3.5 (on average 2.5) months (Table 1). It follows (based on the average week leaf area damaged by male and female imagoes – sex ratio 1:1) that imagoes took

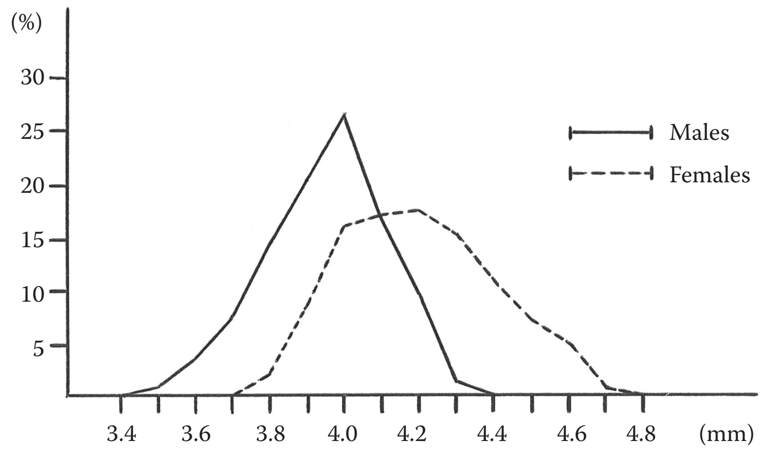

Fig. 4. The body length of imagoes of *P. vitellinae*. Mean length of males is 3.95 mm and of females 4.2 mm

Table 3. Average number (%) of frass pellets produced by imagoes of *P. vitellinae* during particular week intervals. Imagoes were caught at the beginning of the period of feeding on *S. fragilis* in Bílovice nad Svitavou. Laboratory rearings on *S. fragilis*, 2005

Week	Period	Rearing 1		Rearing 2		Rearing 3		Rearing 4		Rearing 5	
		No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
1st	4–10 May	181	8.0	170	7.8	188	5.1	137	4.7	82	6.2
2nd	11–17 May	227	10.1	215	9.8	229	6.2	148	5.1	97	7.3
3rd	18–24 May	387	17.2	405	18.5	396	10.8	259	9.0	221	16.7
4th	25–31 May	240	10.6	214	9.8	270	7.4	191	6.6	151	11.4
5th	1–7 June	189	8.4	121	5.5	284	7.8	0	0	120	9.1
6th	8–14 June	101	4.5	0	0	30	0.8	0	0	95	7.2
7th	15–21 June	29	1.3	0	0	0	0	12	0.4	26	2.0
8th	22–28 June	98	4.3	0	0	0	0	14	0.5	19	1.4
9th	29–5 July	120	5.3	0	0	0	0	66	2.3	31	2.3
10th	6–12 July	186	8.3	99	4.5	164	4.5	244	8.5	187	14.1
11th	13–19 July	244	10.8	168	7.7	220	6.0	238	8.2	82	6.2
12th	20–26 July	168	7.5	160	7.3	368	10.0	312	10.8	106	8.0
13th	27–2 August	82	3.6	139	6.4	387	10.6	234	8.1	104	7.9
14th	3–9 August	2	0.1	109	5.0	350	9.6	192	6.6	2	0.2
15th	10–16 August	–	–	107	4.9	296	8.1	156	5.4	–	–
16th	17–23 August	–	–	130	5.9	299	8.2	212	7.3	–	–
17th	24–30 August	–	–	70	3.2	135	3.7	163	5.6	–	–
18th	31–6 September	–	–	81	3.7	46	1.2	265	9.2	–	–
19th	7–13 September	–	–	–	–	–	–	47	1.6	–	–
20th	14–15 September	–	–	–	–	–	–	2	0.1	–	–
Total		2,254	100.0	2,188	100.0	3,662	100.0	2,892	100.0	1,323	100.0
Number of ♂♂/♀♀		1/1		1/1		1/1		0/2		2/0	
Mean length/width of a frass pellet (mm)		0.8/0.25		0.8/0.24		0.8/0.26		0.9/0.27		0.7/0.23	
Mean volume of one frass pellet (mm^3)		0.03925		0.03617		0.04245		0.05150		0.02901	
Mean volume of frass pellets (mm^3)		88.5		79.1		155.5		148.9		38.4	

food more or less continually in these years (i.e. without long-term interruption). Imagoes damaged on average 19.2 to 36.1 (on average 28.6) cm^2 leaves. Within 1 hour, they damaged 0.1 to 2.7 mm^2 leaves. According to a preliminary investigation carried out by Finet and Gregoire (1981) imagoes

Table 4. Mean number and volume of frass pellets (mm^3) produced by male and female imagoes of *P. vitellinae* (1:1) during feeding in particular months from damaged area of 1 cm^2. Mean volume of one frass pellet = 0.03925 mm^3. Laboratory rearings on *S. fragilis*, 2005

Imagoes	Frass	May	June	July	August	September	October	Mean
After wintering	number	83	95	82	124	147	–	106
	volume	3.3	3.7	3.2	4.8	5.8	–	4.2
1st generation	number	–	64	70	120	133	–	97
	volume	–	2.5	2.7	4.7	5.2	–	3.8
2nd generation	number	–	–	?	107	123	–	115
	volume	–	–	?	4.2	4.8	–	4.5
3rd generation	number	–	–	–	?	105	107	106
	volume	–	–	–	?	4.1	4.2	4.2

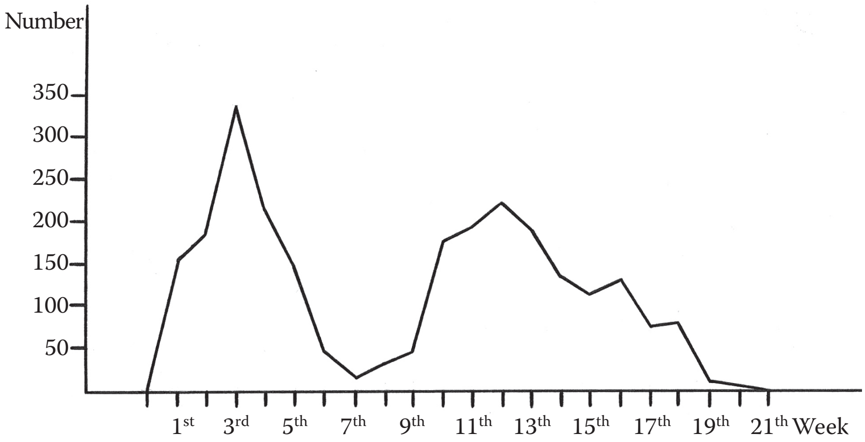

Fig. 5. Mean number of frass pellets produced by imagoes of *P. vitellinae* (sex ratio 1:1) in particular week intervals (after their hibernation in nature). Laboratory rearings on leaves of *S. fragilis*, 2005

feeding on *P. trichocarpa* × *P. deltoides* damaged 2 to 2.5 mm^2 per 1 hour. In an extraordinary warm year 2005, imagoes fell (after 4- to 5-week feeding) into a spring/summer diapause taking about 3 to 5 weeks (Table 2) at the beginning of June. Diapausing imagoes lived 3 to 4 (on average 3.5) months (i.e. by one month longer) and damaged 13.0 to 36.8 (on average 27.2) cm^2 leaves (i.e. roughly the same area as non-diapausing imagoes). Before the diapause, they damaged on average 12.8 cm^2 (47.1%) and after the diapause 14.4 cm^2 (52.9%) (Fig. 3). With respect to on average larger size of females (Fig. 4) and much higher energy expenditures for the creation of eggs the average consumption of food in females is significantly (about 2.4×) higher than in males. Imagoes spend nearly 90% time during food intake (Finet, Gregoire 1981). According to Peacock et al. (2003), there are certain geographical differences in the amount of consumed food in various host plants dimensions and weight of the body (including the percentage of fat in dry matter) being higher in northern localities.

During feeding, imagoes produce 1,323 to 3,662 (on average 2,464) frass pellets of a total volume of 38.4 to 155.5 mm^3 (Table 3). The number and the total volume of male frass pellets ranged in the lower half of the range (in males frass pellets in the upper half). Frass pellets are oblong, cylindrical to fusiform. At first, they are dark green, later dark brown to black. Their mean length is 0.8 mm and width 0.25 mm. Mean dimensions of male frass pellets are 0.7 × 0.23 mm, those of female frass pellets 0.9 × 0.27 mm (Table 3). The mean number and volume of frass pellets defecated by male and female imagoes during particular months (from damage of a size of 1 cm^2) significantly increases in August and September (Table 4). This increase is undoubtedly related to the trophic value of food gradually worsening during the growing season. The course of the defecation of imagoes of a wintering generation (sex ratio 1:1) in particular week intervals in 2005 (i.e. in the year with a month spring/summer diapause) is illustrated in Fig. 5.

Last year's beetles occur on their host plants usually from the end of April to the beginning of September (in the laboratory till mid-August – Fig. 6). It is probable that also in nature beetles can enter the diapause under extremely warm springs and after the change of climatic conditions to continue again in feeding. In such a case, the occurrence of last year's

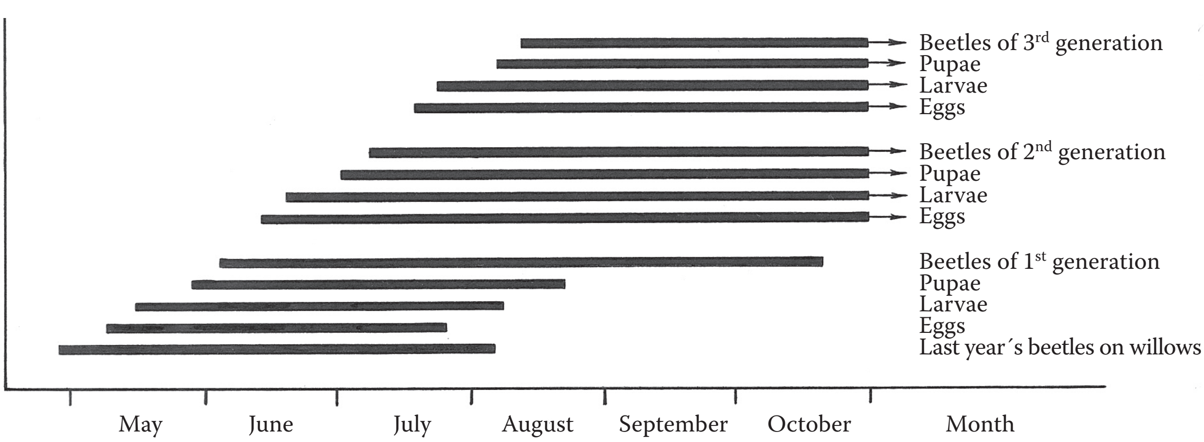

Fig. 6. Basic scheme of the development of *P. vitellinae* on *S. fragilis*. Laboratory rearings, 1999

Table 5. Mean period of feeding of *P. vitellinae* females of particular generations from the beginning of feeding on *S. fragilis* to the beginning of egg laying. Mean period of egg laying and the mean period of life of females (males) of particular generations after the end of oviposition (all in days). Laboratory rearings, 1998–2005

Generation	Mean period		
	of feeding to the beginning of oviposition	of oviposition	of life of ♀♀(♂♂) after the end of oviposition
After wintering (without a spring/summer diapause)	14	57	8 (17)
After wintering (with a diapause)	14 + 5	30 + 48	6 (6)
1st generation	11	30	6 (12)
2nd generation	11	46	3 (?)
3rd generation	(9 + 14)	(57) (after hibernation)	(8/17/)

Table 6. Mean number (%) of eggs laid by females of *P. vitellinae* during particular week intervals. Imagoes were obtained at the beginning of the period of feeding on *S. fragilis* in Bílovice nad Svitavou (in 1999* in Adamov and in 2001 in Žďár nad Sázavou). In dead females, the number of non-laid eggs was found by means of the dissection of ovaries. Laboratory rearings on *S. fragilis*

Week	Period	1998		1999		1999*		2001	
		No.	(%)	No.	(%)	No.	(%)	No.	(%)
1st	4–10 May	22.9	12.1	13.3	5.8	3.5	0.9	–	–
2nd	11–17 May	60.8	32.1	30.5	13.4	13.2	3.3	?	?
3rd	18–24 May	61.6	32.5	42.5	18.7	36.7	9.1	10.0	2.9
4th	25–31 May	31.3	16.5	46.0	20.2	84.3	20.9	42.5	12.5
5th	1–7 June	6.6	3.5	29.8	13.1	74.3	18.5	39.0	11.4
6th	8–14 June	4.6	2.4	29.2	12.9	66.5	16.5	49.6	14.6
7th	15–21 June	1.4	0.7	23.5	10.3	60.8	15.1	50.2	14.7
8th	22–28 June	0.5	0.2	9.3	4.1	29.3	7.3	38.2	11.2
9th	29–5 July	0	0	1.3	0.6	23.3	5.8	37.7	11.1
10th	6–12 July	–	–	0	0	7.8	1.9	35.0	10.3
11th	13–19 July	–	–	2.0	0.9	2.8	0.7	25.0	7.3
12th	20–26 July	–	–	0	0	0	0	10.5	3.1
13th	27–2 August	–	–	–	–	0	0	3.0	0.9
14th	3–9 August	–	–	–	–	0	0	0	0
15th	10–16 August	–	–	–	–	–	–	0	0
Laid		189.7	100.0	227.4	100.0	402.5	100.0	340.7	100.0
Non-laid		1.3	–	4.0	–	6.0	–	1.0	–
Total		191.0	–	231.4	–	408.5	–	341.7	–
Number of ♂♂/♀♀		8/8	–	10/6	–	4/6	–	3/4	–

beetles on trees could extend until the beginning of October.

Egg laying of the 1st generation

Eggs are created in meroistic ovarioles of a telotrophic type, viz only during feeding. There are 20 ovarioles in ovaries, i.e. 10 in each of the ovaries (Zachvatkin 1967). After about one-week feeding, imagoes mate on leaves for the first time and after next week females lay the first eggs (Table 5). Females which did not mate in spring lay always unfertilized eggs. Kendall and Wiltshire (1998) came to the same conclusion in a related *P. vulgatissima*.

In localities under study, the first eggs of the first generation were found about 6 May. In the period of the most intensive egg laying (in the 2nd half of May and in June), females lay eggs nearly every day. In the laboratory, females (without the spring/summer diapause) mated repeatedly and laid eggs for a period of almost 2 months. Females with the diapause reproduced for a period of 2.5 months (of this

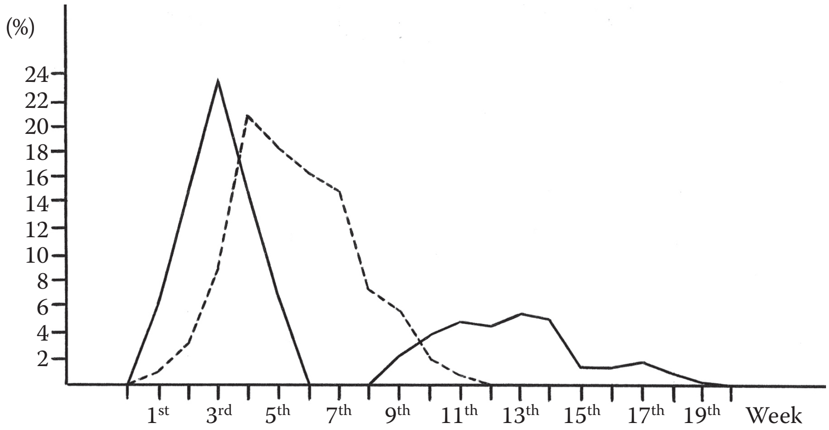

Fig. 7. The course of egg laying by females of *P. vitellinae* in particular week intervals (after their hibernation in nature). Laboratory rearings on leaves of *S. fragilis*, 1999 (dash line), 2005 (solid line)

1 month before the diapause and 1.5 months after the diapause) (Tables 6 and 7, Fig. 7). Male imagoes (without a diapause) lived in captivity on average 69 (female 57) days. Male imagoes (with a diapause) lived on average 93 (female 100) days (Table 8). Several days after the termination of egg laying imagoes died (Table 5). Males in rearings quaintly tried to copulate even with dead females.

Females place eggs into 8- to 20-member groups on the abaxial face of leaves (Figs. 8 and 9). The majority of eggs (about 52%) is laid on the basal third of a leaf blade (Fig. 10). A group of eggs of a medium size is laid within 30 min. In laboratory rearings, females of a wintering generation laid only about 43% eggs on the abaxial face of leaves. Almost 45% eggs were laid on glass walls (mainly on caps) of rearing

Table 7. Mean number (%) of eggs laid by females of *P. vitellinae* during particular week intervals. Imagoes were obtained at the beginning of the period of feeding on *S. fragilis* in Bílovice nad Svitavou. In dead females, the number of non-laid eggs was found by means of the dissection of ovaries. Laboratory rearings on *S. fragilis*, 2005

Week	Period	Rearing 1		Rearing 2		Rearing 3		Rearing 4	
		No.	(%)	No.	(%)	No.	(%)	No.	(%)
1st	4–10 May	37	6.9	30	11.6	17	3.6	16.5	6.1
2nd	11–17 May	87	16.2	54	20.9	54	11.3	36.0	13.3
3rd	18–24 May	120	22.3	101	39.2	96	20.2	47.0	17.4
4th	25–31 May	101	18.8	63	24.4	61	12.8	5.0	1.9
5th	1–7 June	47	8.7	10	3.9	47	9.9	0	0
6th	8–14 June	0	0	0	0	0	0	0	0
7th	15–21 June	0	0	0	0	0	0	0	0
8th	22–28 June	0	0	0	0	0	0	0	0
9th	29–5 July	36	6.7	0	0	0	0	0	0
10th	6–12 July	43	8.0	0	0	8	1.7	14.5	5.4
11th	13–19 July	36	6.7	0	0	25	5.3	17.0	6.3
12th	20–26 July	17	3.1	–	–	30	6.3	26.5	9.8
13th	27–2 August	14	2.6	–	–	42	8.8	29.5	10.9
14th	3–9 August	0	0	–	–	62	13.1	18.5	6.9
15th	10–16 August	–	–	–	–	6	1.3	16.0	5.9
16th	17–23 August	–	–	–	–	7	1.5	15.0	5.5
17th	24–30 August	–	–	–	–	20	4.2	13.0	4.8
18th	31–6 September	–	–	–	–	–	–	11.5	4.3
19th	7–13 September	–	–	–	–	–	–	4.0	1.5
20th	14–15 September	–	–	–	–	–	–	0	0
Laid		538	100.0	258	100.0	475	100.0	270	100.0
Non-laid (mean)		8	–	0	–	4	–	3	–
Total		546	–	258	–	479	–	273	–
Number of ♂♂/♀♀		1/1		1/1		1/1		0/2	

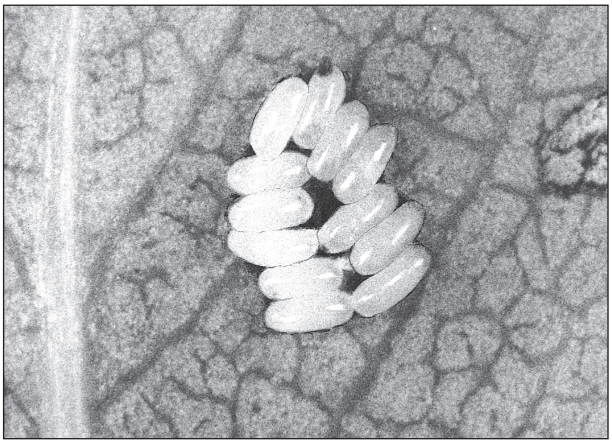

Fig. 8. Egg-laying of *P. vitellinae* on the abaxial face of leaves of *S. fragilis*. Bílovice nad Svitavou, 15 May 1999

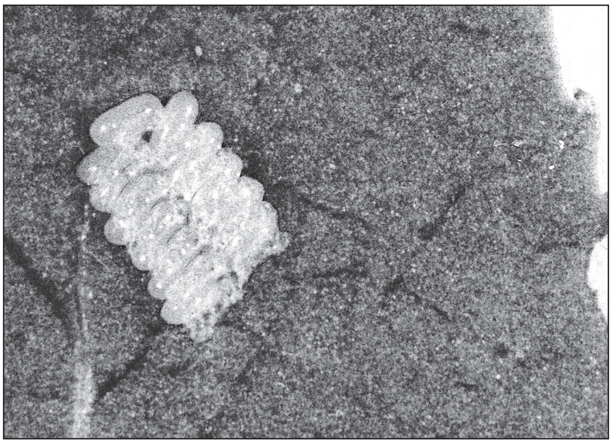

Fig. 9. Egg-laying of *P. vitellinae* on the abaxial face of leaves of *S. fragilis*. Eggs are covered on their surface by the secretion of accessory glands. Bílovice nad Svitavou, 11 May 1998

plates and 12% on the adaxial face of leaves (Table 9). In particular rearings, females laid eggs either individually or in small groups (on average 3.4 eggs each) (Table 10).

Eggs of *P. vitellinae* are oval, grey-white to yellowish and glossy. Newly hatched eggs are 0.86 mm long and 0.43 mm wide, sticky on their surface. By means of an air-stiffening thickening secretion the eggs are stuck to a leaf, namely always flat, to serried double series with poles close to each other. The whole group of eggs is often covered with a thin transparent cuticle created by the stiffened secretion of accessory glands (Fig. 9). The cuticle cleaves closely on a chorion and sometimes partly passes to a leaf. During a one-week embryonal development in the laboratory, the mean length of eggs increases to 0.97 mm and width to 0.47 mm (Table 11, Fig. 11). Larvae usually do not hatch from eggs laid on walls of plates. It means that the close contact of eggs with the abaxial surface of the living leaf blade significantly stimulates the embryonal development. On the other hand, Zachvatkin (1967) claims that embryos allegedly develop even without additional moistening in eggs stuck on glass or miller silk. In rearings of imagoes, cannibalism which showed itself in the consumption of less than 3% eggs was observed only rarely (Table 12).

Table 8. Mean period of life of male and female imagoes of wintering generations of *P. vitellinae* without a spring/summer diapause and with the diapause (days). Imagoes were caught on 4 May in Bílovice nad Svitavou (in 2001 on 18 May in Žďár nad Sázavou). The table also gives the mean number of laid eggs and the mean area of damaged leaves. Laboratory rearings on *S. fragilis*

Sex/Number	Imagoes without a spring/summer diapause				Imagoes with a diapause
	1998	1999	2001	Mean	2005
Males	51	71	84	69	93
Females	44	53	75	57	100
Mean	48	62	79	63	96
Number of eggs	190	315	342	282	385
Damaged area (cm^2)	19.2	22.3	34.2	25.2	27.2

Table 9. Localization of eggs of the 1st and 2nd generations of *P. vitellinae* on leaves of *S. fragilis* and on walls of rearing vessels. Laboratory study, 1998–2005

Localization	Eggs of the 1st generation		Eggs of the 2nd generation	
	No.	(%)	No.	(%)
Abaxial leaf face	3,085	42.9	1,420	63.0
Adaxial leaf face	882	12.2	298	13.2
Walls of rearing vessels	3,232	44.9	537	23.8
Total	7,199	100.0	2,255	100.0

Table 10. Numerical proportion (%) of groups with the various number of eggs laid by females of *P. vitellinae* after wintering and by females of the 1st generation. Laboratory rearings on *S. fragilis*, 1998–2001

Number of eggs in a group	Imagoes after wintering		Imagoes of the 1st generation	
	number of groups	(%)	number of groups	(%)
1	742	49.4	23	17.6
2	200	13.3	11	8.4
3	104	6.9	17	13.0
4	87	5.8	19	14.5
5	61	4.1	16	12.2
6	70	4.7	15	11.5
7	48	3.2	10	7.6
8	34	2.2	4	3.0
9	31	2.1	8	6.1
10	30	2.0	2	1.5
11	20	1.3	2	1.5
12	22	1.5	1	0.8
13	10	0.7	1	0.8
14	10	0.7	–	–
15	5	0.3	–	–
16	12	1.0	2	1.5
17	1	–	–	–
18	9	0.6	–	–
19	1	–	–	–
20	–	–	–	–
21	2	0.1	–	–
22	1	–	–	–
23	–	–	–	–
24	–	–	–	–
25	2	0.1	–	–
Total	1,502	100.0	131	100.0

Based on laboratory studies the fecundity of females of the wintering generation of *P. vitellinae* on *S. fragilis* amounts to 191 to 546 (on average 341) eggs. Females which did not enter the spring/summer diapause laid 191 to 546 (on average 293) eggs (Table 6). Females which underwent a diapause laid 258 to 546 (on average 389) eggs. Before the diapause, they laid about 67% eggs and after the diapause about 33% eggs (Table 7). Ovaries of 52% naturally died females did not contain any developed eggs. In total 48% died females showed ovaries with 1 to 18 (on average 3) unlaid eggs.

There are very few more accurate literature data on egg laying and fecundity of *P. vitellinae.* For example, according to Kaltenbach (1874), there are 13 to 18 eggs in groups, according to Blunck et al. (1954) and Schnaider (1957) 10 to 30 eggs, according to Escherich (1923), Živojinovič (1948), etc. about 20 eggs and according to Zachvatkin (1967) 8 to 36 eggs. The same number of eggs in groups (8 to 20) as this paper author gives Gäbler (1955). Kendall and Wiltshire (1988) found that in clutches of a related species *P. vulgatissima* there were on average only 10.2 eggs. According to available literature, females lay in total 200 to 300 eggs. Thus, based on our study, the average fecundity of females on *S. fragilis* (about 341 eggs) is significantly (on average 1.4 times) higher.

It is known that imagoes of *P. vitellinae* prefer newly unfolded leaves near shoot tops while eggs of the chrysomelid are mostly laid on somewhat older leaves in proximal parts of shoots. According to Rowell-Rahier (1984a) females also sometimes lay eggs on old leaves at bases of shoots. Females are very movable and after laying one clutch (which takes only a short time) they quickly leave the lower space of shoots (Finet, Gregoire 1981). The marginalization of young leaves during egg laying limits

Table 11. Length and width of eggs of *P. vitellinae* during embryonal development (mm). Laboratory rearing, 1998–2005

Eggs	Length		Width	
	from–to	mean	from–to	mean
Immediately after egg-laying	0.78–0.93	0.86	0.39–0.46	0.43
In the half of an embryonal development	0.85–0.97	0.91	0.41–0.48	0.45
Immediately before hatching	0.93–1.00	0.97	0.44–0.50	0.47
Total	0.78–1.00	0.91	0.39–0.50	0.45

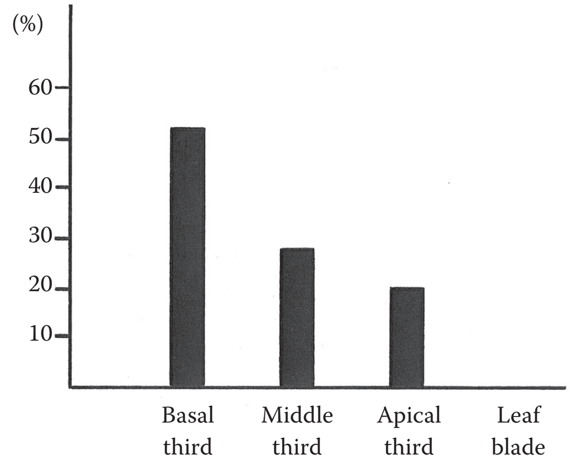

Fig. 10. Localization of eggs of *P. vitellinae* on the abaxial face of leaves of *S. fragilis*. Laboratory rearings, 1998, 1999

Table 12. Mean mortality of eggs (in % of the total number of eggs) caused by imagoes of *P. vitellinae* in common rearings of individuals of both sexes on leaves of *S. fragilis*. Laboratory rearings, 1998–2005

Number of imagoes	Eggs of the 1st generation	Eggs of the 2nd and 3rd generations
≤ 5	0.6	1.4
6–10	6.8	1.2
≥ 11	1.0	1.8
Total	2.8	1.5

feeding competition between imagoes and larvae and evidently also significantly decreases mortality caused by various (particularly insect) predators and parasitoids.

Development of the 1st generation

After 8 to 11 days (according to Schnaider 1957 after 1 to 2 weeks) following the oviposition, egg envelopes crack at the cranium pole by a lengthwise fissure (reaching up to the half of the egg length) and egg larvae gradually hatch. In the laboratory, larvae hatched as early as after 6 to 7 days (Fig. 11). Newly hatched larvae are about 1.1 mm long, yellowish, with black head and legs. Their cranium is 0.39 to 0.46 mm wide (Fig. 12). During 2 to 3 hours, they show dye and then concentrate in the immediate vicinity of abandoned egg envelopes (Fig. 13). Newly hatched larvae never consume empty egg envelopes (as against larvae of *Plagiodera versicolora, Chrysomela populi,* etc.). They line closely side by side and soon begin jointly to skeletonize leaves. During this "frontal feeding", they bite out minute irregular holes of an average length 0.3 mm and width 0.2 mm into leaf blades (Fig. 14). The holes usually reach up

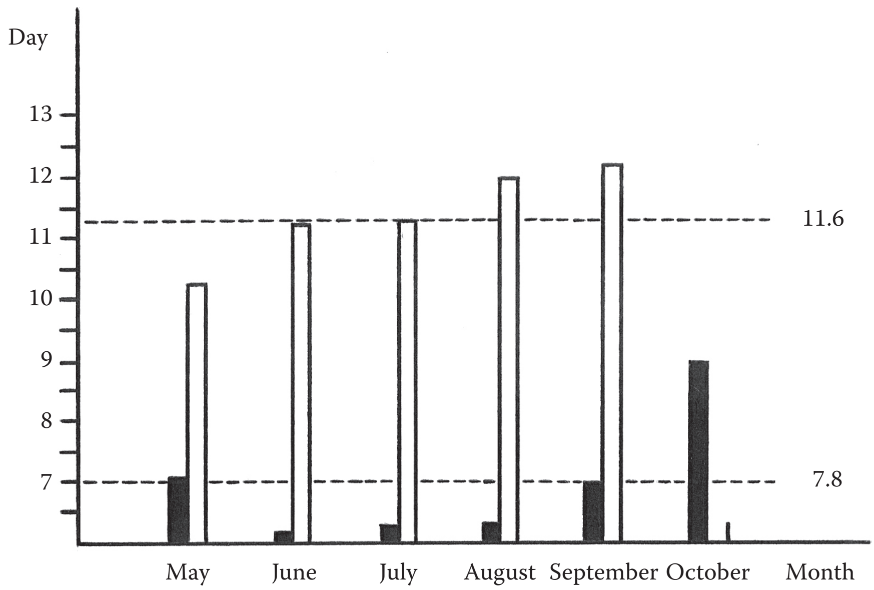

Fig. 11. The mean period of embryonal development (dark columns) and the mean period of development of *P. vitellinae* from the end of feeding of larvae till the occurrence of imagoes on trees (light columns). Laboratory rearings on leaves of *S. fragilis*, 1999, 1999, 2001 and 2005

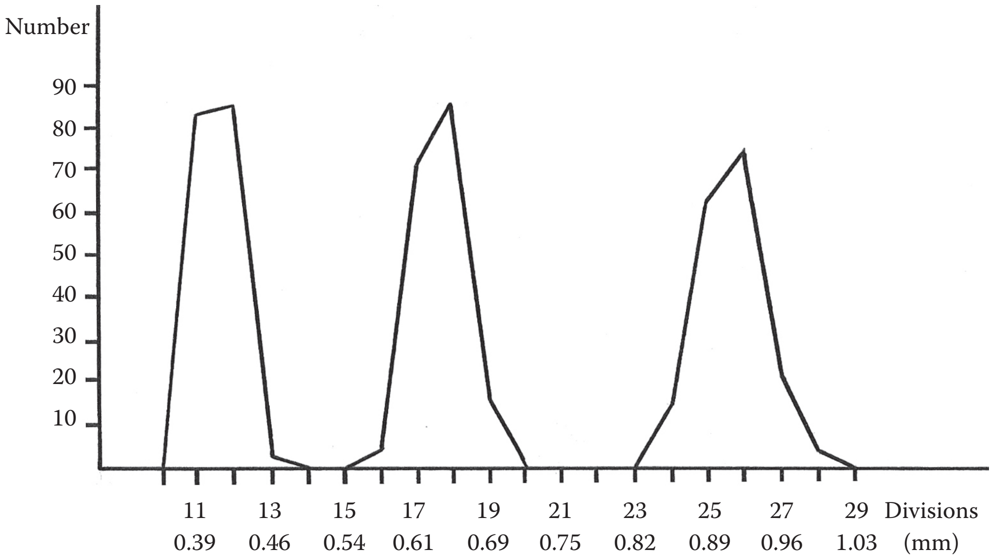

Fig. 12. The width of cranium of larvae of the 1st to the 3rd instar of *P. vitellinae* (1 division = 0.0357 mm)

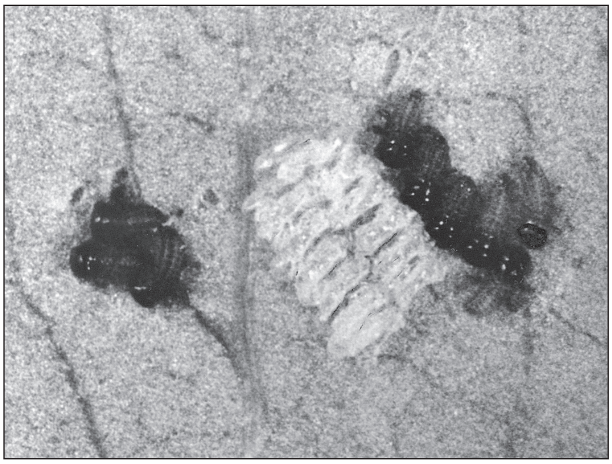

Fig. 13. Larvae of the 1st instar of *P. vitellinae* soon after hatching from eggs on the abaxial face of leaves of *S. fragilis*. Bílovice nad Svitavou, 22 May 1998

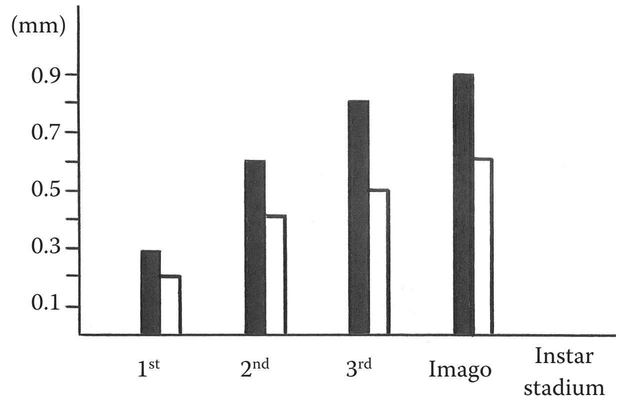

Fig. 14. Mean length of feeding marks (dark columns) and the width of feeding marks (light columns) of larvae of particular instars and imagoes of *P. vitellinae* on leaves of *S. fragilis* (mm). Laboratory rearings, 1998 to 2005

Table 13. Mean period of the development of larvae of the 1st to the 3rd instar of *P. vitellinae* on *S. fragilis* (in dyas and %). A period is given from hatching of larvae from eggs to the end of feeding. Laboratory rearings, 1998–2005

Instar	Period of development				Mean	(%)
1st	4.0	4.5	4.8	5.0	4.6	34.1
2nd	3.5	3.7	4.0	4.5	3.9	28.9
3rd	4.5	4.8	5.2	5.5	5.0	37.0
Mean	12.0	13.0	14.0	15.0	13.5	100.0

Table 14. Mean leaf area of *S. fragilis* damaged by larvae of the 1st to the 3rd instar of *P. vitellinae* during May to September. Laboratory rearings, 2005

Instar	May		June		July		August		September	
	(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)	(cm^2)	(%)
1st	0.2	7	0.2	7	0.2	4	0.2	5	0.2	6
2nd	0.5	18	0.5	17	0.7	12	0.6	16	0.6	17
3rd	2.1	75	2.2	76	4.7	84	3.0	79	2.7	77
Total	2.8	100	2.9	100	5.6	100	3.8	100	3.5	100

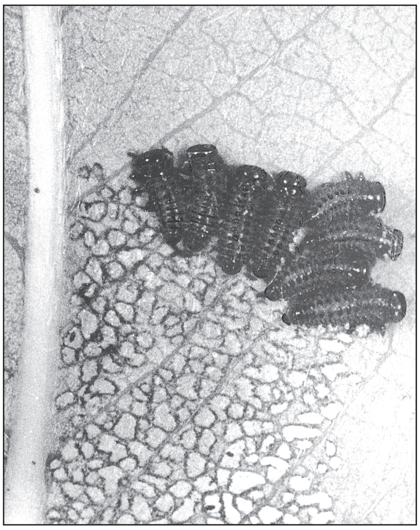

Fig. 15. Larvae of the 1st instar of *P. vitellinae* during feeding on the abaxial face of leaves of *S. fragilis*. Bílovice nad Svitavou, 25 May 1998

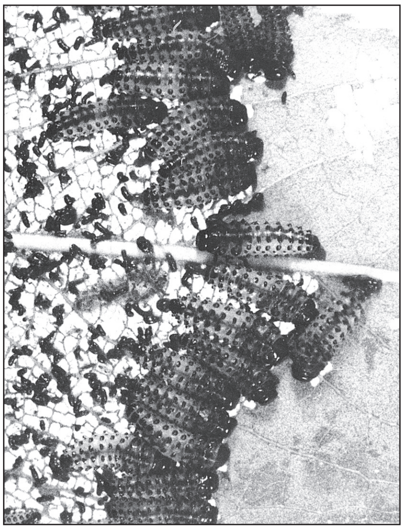

Fig. 16. Larvae of the 2nd instar of *P. vitellinae* during feeding on the abaxial face of leaves of *S. fragilis*. Laboratory rearings, 4 June 1998

Fig. 17. Abaxial face of leaves of *S. fragilis* damaged by larvae of the 2nd instar of *P. vitellinae*. Laboratory rearings, 31 May 1998

to the upper epidermis not disturbing the epidermis, leaf veins and vein anastomoses. Part of the leaf blade (about 20%) between particular feeding marks remains undamaged (Fig. 15). During 4.5 days, larvae reach a length of 2 mm (Table 13). Within the period, they damage on average 0.2 cm^2 leaf blade of *S. fragilis* (Table 14). They produce on average 109 fusiform frass pellets of a mean length of 0.18 mm and width 0.07 mm (Tables 15 and 16). Grown up larvae of the 1st instar gradually leave the front of feeding larvae roughly 3 hours before ecdysis. Through the terminal part of their abdomen they attach themselves to the undisturbed part of the leaf blade. The ecdysis of larvae takes about 15 to 20 minutes.

The cranium of larvae of the 2nd instar is 0.57 to 0.69 mm wide and the length of the larvae is 1.5 to 3.8 (on average 2.6) mm (Fig. 12). After about 2 hours of rest, newly hatched larvae begin to feed on the abaxial face of leaves. For a period of about 4 days, they jointly frontally bite out holes 0.6 × 0.4 mm (Table 13, Figs. 14 and 16). They damage on average 0.5 cm^2 leaf blades of *S. fragilis* and exclude on average 168 fusiform frass pellets of a dimension about 0.36 × 0.13 mm (Tables 14 to 16). They do not damage leaf venation and upper epidermis, however, they consume all leaf parenchyma (Fig. 17). Grown up larvae of the 2nd instar hatch on the abaxial face of leaves (near the place of feeding).

Larvae of the 3rd (i.e. last) instar show cranium 0.86 to 1 mm wide and the length of the larvae is 3.4 to 6.2 (on average 5) mm (Fig. 12). For a period of on average 5 days, they bite out holes about 0.9 × 0.6 mm (Table 13, Figs. 14 and 18) either jointly or in small close groups. They damage on average 2.1 cm^2 leaf blades of *S. fragilis* and exclude on average 335 fusiform frass pellets of an average dimension of 0.5 × 0.18 mm (Tables 14 to 16, Fig. 19). Also larvae of the 3rd instar skelotonize leaves from the abaxial face (in the laboratory, however, also from the adaxial face) and leave both the upper epidermis and venation intact. If we displace young larvae of the 3rd instar to the adaxial face of leaves then 80% larvae begin to skelotonize leaves from this face and about 20% larvae move to the abaxial face.

Table 15. Mean number and volume of frass pellets produced by larvae of the 1st to the 3rd instar of *P. vitellinae* during May to September. Mean volume of frass pellets from 1 cm^2 damaged leaf area (mm^3/cm^2). Laboratory rearings, 2005

Instar	May		June		July		August		September	
	No.	(mm^3)	No.	(mm^3)	No.	(mm^3)	No.	(mm^3)	No.	(mm^3)
1st	109	0.07	104	0.07	130	0.09	133	0.09	166	0.10
2nd	168	0.80	161	0.77	259	1.24	237	1.13	310	1.48
3rd	335	4.35	335	4.34	616	7.99	584	7.58	618	8.02
Total	612	5.22	600	5.18	1,005	9.32	954	8.80	1,094	9.60
(mm^3/cm^2)	–	1.90	–	1.80	–	1.70	–	2.30	–	2.70

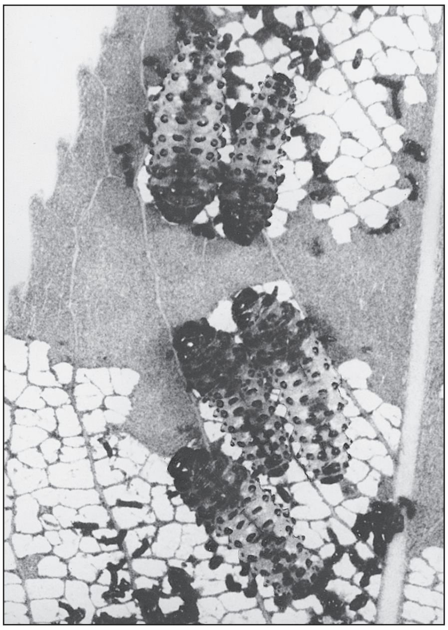

Fig. 18. Larvae of the 3rd instar of *P. vitellinae* during feeding on the abaxial face of leaves of *S. fragilis*. Laboratory rearings, 11 June 1998

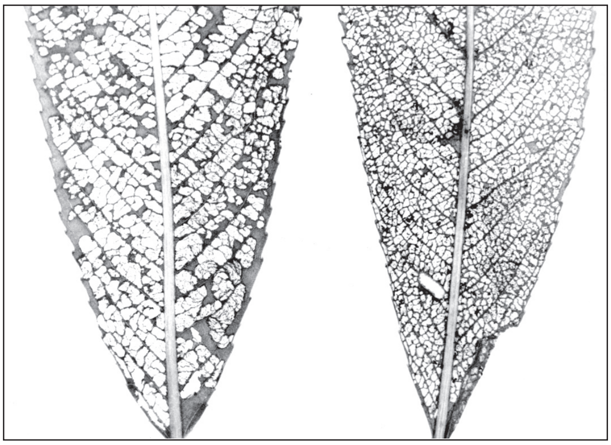

Fig. 19. Abaxial face of leaves of *S. fragilis* damaged by larvae of the 3rd instar of *Lochmaea capreae* (L.) (left) and *P. vitellinae* (right). Laboratory rearings, 8 June 1996

The first generation o larvae occurs in nature usually from the 2nd decade of May to mid-August (at a supposed spring/summer diapause probably till mid-September). The development of larvae (from hatching from eggs till a departure to the earth) takes 2 to 3 weeks, in the laboratory 12 to 13 days (Table 13, Fig. 20). Also SCHNAIDER (1957) mentions the 2–3-week development of larvae. Within the period, larvae damage in total 2.8 to 5.6 (on average 4) cm^2 leaves of *S. fragilis* , i.e. on average 7.4 times less than last year's imagoes after wintering (Table 14). Of the total damaged area larvae of the 1st instar damaged about 6%, larvae of the 2nd instar about 16% and larvae of the 3rd instar about 78% (Fig. 21). During feeding in May and June, larvae produce about 600 frass pellets, in July about 1,000 frass pellets

Table 16. Mean dimensions and volume of frass pellets defecated by larvae of the 1st to the 3rd instar and imagoes of *P. vitellinae*. Laboratory rearings on *S. fragilis*, 1998–2005

Instar	Length (mm)	Width (mm)	Volume (mm^3)
1st	0.18	0.07	0.00069
2nd	0.36	0.13	0.00477
3rd	0.51	0.18	0.01297
Imago	0.80	0.25	0.03925

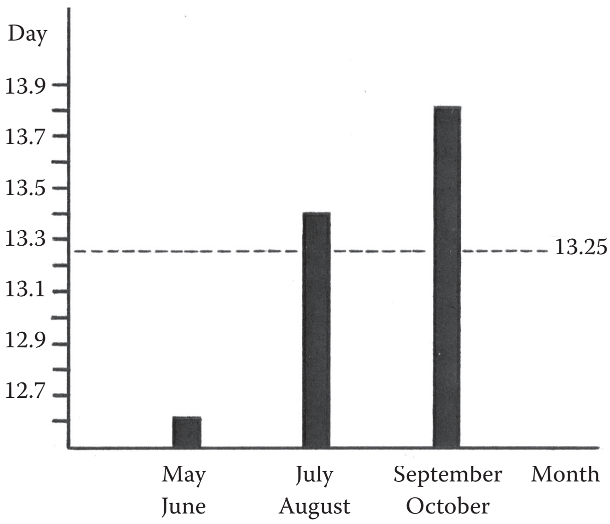

Fig. 20. The mean period of development of larvae of *P. vitellinae* from hatching to the end of feeding the larvae (in days). Laboratory rearings on leaves of *S. fragilis*, 1998 to 2005

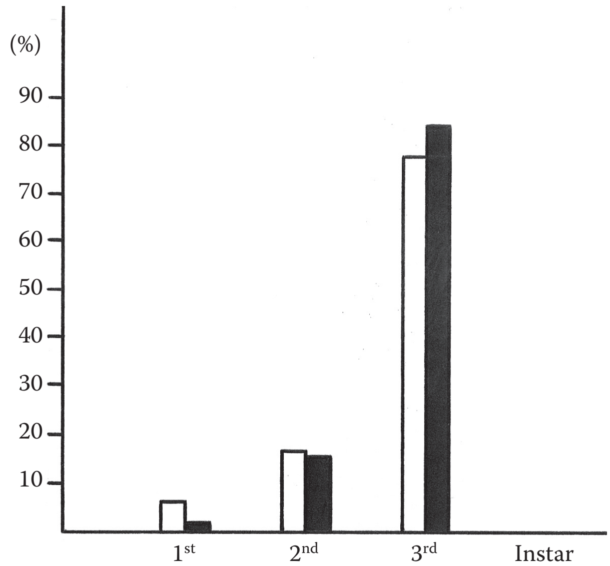

Fig. 21. Leaf area of *S. fragilis* (in % of the total damaged area) damaged by larvae of the 1st to the 3rd instar of *P. vitellinae* (light columns). Dark columns depict the volume of frass pellets (in % of the total frass pellets volume). Laboratory rearings, 2005

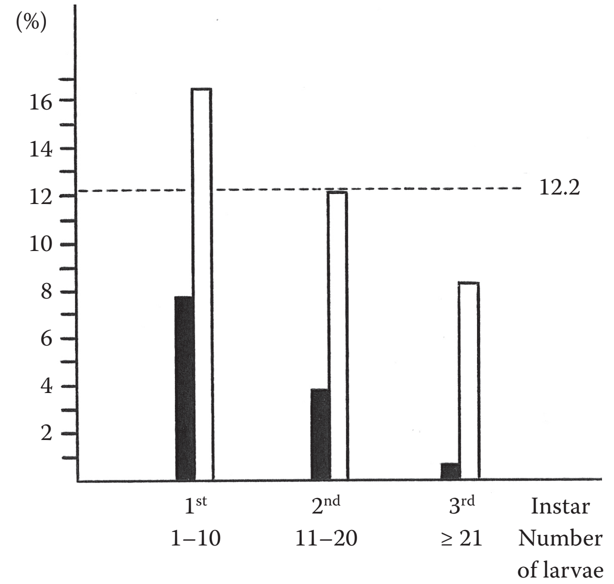

Fig. 22. Mortality of particular instars of larvae (dark columns) and the total mortality of larvae of *P. vitellinae* in relation to the number of larvae in a group (light columns) (in %). The mean mortality of larvae is depicted by a dash line. Laboratory rearings on leaves of *S. fragilis*, 1998, 1999, 2001 and 2005

Fig. 23. Pupae of *P. vitellinae* in earth pupal chambers. Laboratory rearings, 8 June 1998

(Table 15). In rearings, on average 12.2% larvae died and the highest mortality showed larvae of the 1st instar (Fig. 22). With the increasing number of larvae in groups the mortality of larvae significantly decreased.

Larvae of *P. vitellinae* live gregariously in stable close groups. Gregariousness facilitates the use of food sources (particularly in the initial period of feeding) and significantly strengthens the active and passive protection of larvae from natural enemies. As already mentioned the abundance of gregariously living larvae is in positive correlation with the high content of some phenolic glucosides and the low density of trichomes on the abaxial face of leaves. Glucosides (particularly salicin and salicortin) are used by larvae for the formation of salicylaldehyde which is the main compound of the defensive secretion of larvae secreted by eversible dorsal glands (Soetens, Pasteels 1988; Soetens et al. 1991, etc.). However, high concentrations of usual phenolic glucosides in leaves function on some other insect herbivores (e.g. *P. vulgatissima* and *Galerucella lineola*) as repellents (Kendall et al. 1996).

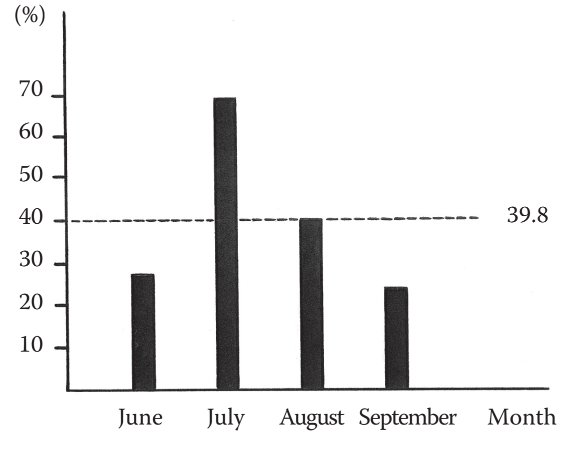

Fig. 24. Mortality of prepupae, pupae and imagoes of *P. vitellinae* during their development in soil. Mean mortality is depicted by a dash line. Laboratory rearings, 2005

Grown up larvae of the 3rd instar hide in the earth in the vicinity of host species. There, they create an oval pupal chamber with smoothed walls in the surface layer of soil (at a depth of 1 to 4 cm). In the chamber, they prepare about 4 days (in the laboratory 2.5 days) for pupation. The stage of a pupa (Fig. 23) takes about 8 days (in the laboratory 5.5 to 6 days) after which imagoes hatch. Imagoes remain in chambers about 4 days (in the laboratory 2.5 days) and then climb from soil and appear on host trees. In nature, imagoes of the 1st generation appear in the open after 2 to 3 weeks (in the laboratory after 10 to 12 days) after the termination of feeding (Fig. 11). Prepupae, pupae and young off-colour imagoes in pupal chambers are very sensitive to adequate soil moisture, structure and acidity. In excessively moist soil, they pupate at the very surface of soil (in the laboratory even on the surface) and in the acid humous soil mostly die. Also young imagoes can die in too dry and hard pupal chambers. Imagoes fail to bite out from them. In the laboratory, on aver-

Table 17. Mean leaf area of *S. fragilis* (cm^2) damaged by imagoes of the 1^{st} generation of *P. vitellinae* and the mean number of laid eggs in particular week intervals. Imagoes were reared in the laboratory from eggs laid by females after wintering. Laboratory rearings, 1998, 1999

Week	1998		1999								
	9 ♂♂/8 ♀♀		2 ♂♂/6 ♀♀		2 ♂♂/3 ♀♀		3 ♂♂/6 ♀♀		9 ♂♂/8 ♀♀		5 ♂♂
	(cm^2)	No.	(cm^2)	No.	(cm^2)	No.	(cm^2)	No.	(cm^2)	No.	(cm^2)
1^{st}	5.3	0	3.9	0	3.6	0	2.4	0	3.6	0	3.3
2^{nd}	4.2	25.8	4.9	20.0	3.2	25.0	2.8	24.3	4.4	41.9	1.7
3^{rd}	2.6	22.9	4.6	49.7	3.4	52.7	1.6	31.7	4.3	64.1	1.0
4^{th}	1.4	16.8	3.3	45.0	3.2	68.3	1.0	12.2	4.8	71.5	1.3
5^{th}	1.0	7.3	2.0	21.3	2.8	41.0	0	0	3.5	38.5	1.9
6^{th}	0.3	1.1	1.2	6.7	0	0	–	–	1.6	18.5	1.7
7^{th}	0.1	0	0.9	5.0	–	–	–	–	0.5	0	1.7
8^{th}	0	0	0.6	0	–	–	–	–	0.1	0	1.4
9^{th}	–	–	0	0	–	–	–	–	–	–	1.2
10^{th}	–	–	–	–	–	–	–	–	–	–	0.6
11^{th}	–	–	–	–	–	–	–	–	–	–	0.6
12^{th}	–	–	–	–	–	–	–	–	–	–	0
Total	14.9	73.9	21.4	147.7	16.2	187.0	7.8	68.2	22.8	234.5	16.4
Period	15 June– 4 August		19 June– 14 August		19 June– 27 July		22 June– 21 July		26 June– 18 August		26 June– 11 September

age 20% (in 2005 some 40%) prepupae, pupae and imagoes died in soil (Fig. 24).

The development of other generations

P. vitellinae has usually 2 generations in the region of the CR. In southern and central Moravia, imagoes of the 1^{st} generation occur on trees from mid-June to the end of the growing season. Abundance of imagoes increases till the end of August and then gradually decreases. In the laboratory, the first imagoes of the generation were reared usually at the beginning of June. Last imagoes survived in captivity sometimes till the end of October or the beginning of November (Fig. 6). After reaching host species imagoes begin to feed on young leaves of growing shoots. About after 2-week intensive feeding at the end of which imagoes mate for the first time (in the laboratory already after 10 to 12 days), the period of oviposition of the 2^{nd} generation follows (Table 5).

Table 18. Mean leaf area of *S. fragilis* (cm^2) damaged by imagoes of the 1^{st} generation of *P. vitellinae* in particular week intervals. Mean number of frass pellets produced by imagoes and the mean number of eggs laid by females in particular week intervals. Imagoes were reared in the laboratory from eggs laid by females after wintering. Laboratory rearings, 2005

Week	4 ♂♂/4 ♂♂			1 ♀			2 ♀♀			2 ♂♂	
	(cm^2)	frass pellets	eggs	(cm^2)	frass pellets	eggs	(cm^2)	frass pellets	eggs	(cm^2)	frass pellets
1^{st}	3.0	186	0	7.0	448	0	2.2	186	0	2.1	190
2^{nd}	3.9	254	46	8.4	437	80	1.6	127	0	1.6	119
3^{rd}	3.9	258	72	8.8	475	95	4.6	267	1	1.9	167
4^{th}	2.9	195	56	7.9	481	114	4.3	388	29	2.4	223
5^{th}	1.6	107	23	6.4	448	86	2.1	261	22	0.7	90
6^{th}	0.3	26	3	6.5	422	55	0.8	115	4	–	–
7^{th}	0.2	20	–	1.9	176	49	0.7	115	3	–	–
8^{th}	0.2	18	–	0.5	36	8	0.2	34	0	–	–
9^{th}	0	3	–	–	–	–	–	–	–	–	–
Total	16.0	1,067	200	47.4	2,923	487	16.5	1,493	59	8.7	789
Period	9 June–5 August			9 June–1 August			1 July–23 August			30 June–1 August	

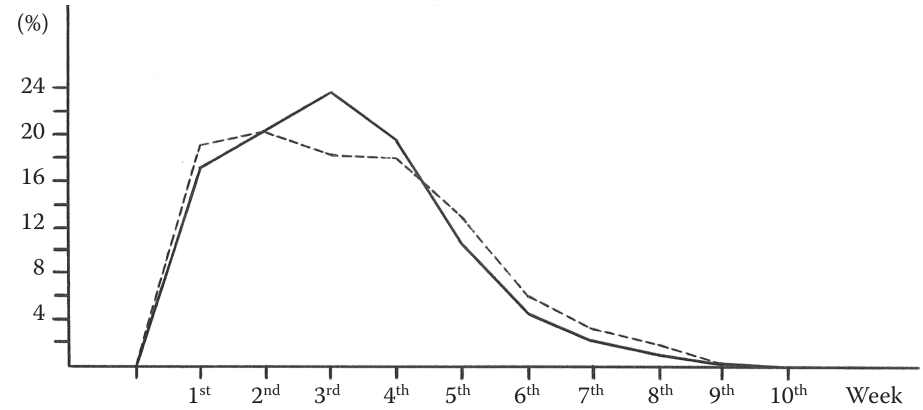

Fig. 25. The course of damage to leaves of *S. fragilis* by imagoes of the 1st generation of *P. vitellinae* (sex ratio 1:1) in % of the total damaged area. Laboratory rearings, 1999 (dash line), 2005 (solid line)

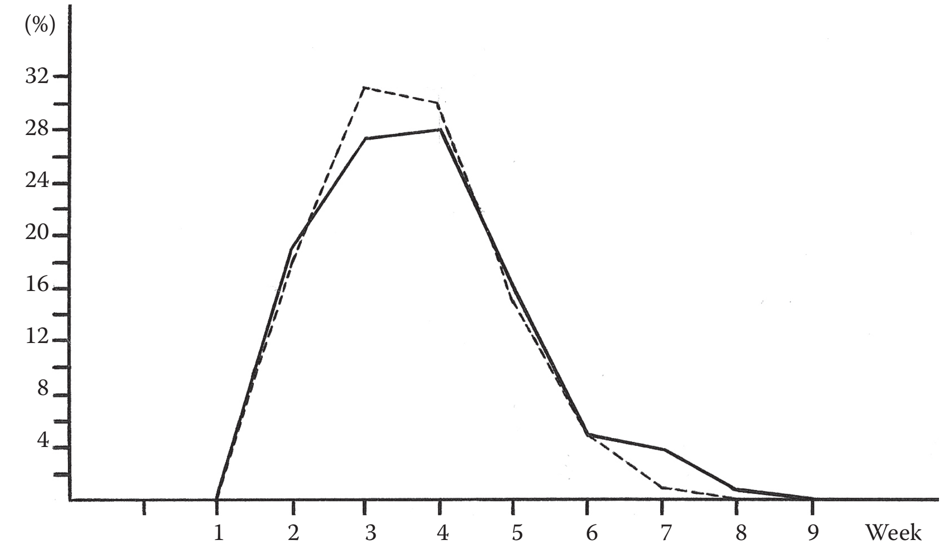

Fig. 26. The course of egg laying by females of the 1st generation of *P. vitellinae* during feeding on leaves of *S. fragilis* (in % of the total number of laid eggs). Laboratory rearings, 1999 (dash line), 2005 (solid line)

Imagoes of the 1st generation lived in captivity on average 55 days. Males lived on average 6 days longer than females. In total, imagoes damaged 8.7 to 47.4 (on average 18.8) cm^2 leaves of *S. fragilis* (Tables 5, 17, 18, Fig. 25). Males damaged on average 2.5 times smaller leaf area than females. Compared to imagoes of a wintering generation (caught after the end of hibernation) which damaged on average 28.6 cm^2 leaves average damage caused by imagoes of the 1st generation (reared in the laboratory) was 34% smaller. Smaller average consumption was obviously caused by the laboratory environment where the development of the chrysomelid proceeded from eggs up to imagoes.

Females of the 1st generation reared in the laboratory already from the stage of eggs laid eggs for a period of 28 to 40 (on average 35) days. The eggs were laid in groups of 1 to 16 pieces, on average 4.7 pieces (Table 10). About 6 days after oviposition females died (Table 5). Fecundity of females amounted to 59 to 487 (on average 182) eggs, i.e. almost 1.9 times lower than in females of a wintering generation caught in nature (Tables 17 and 18, Fig. 26). Imagoes of the 1st generation produced from 1 cm^2 damaged area on average 97 frass pellets of a total volume of 3.8 mm^3, i.e. on average 9 frass pellets less than imagoes after hibernation (Table 4). Average number and the total volume of frass pellets produced from 1 cm^2 damaged leaf area gradually increased up to double during June to September. On the basis of these results it is possible to suppose that the effectiveness of using food by imagoes of the 1st generation decreased by 50% during the time due to the decrease of the food nutritional value.

From eggs of the 2nd generation laid by females of the 1st generation at the end of June, in July and August, larvae hatched after 8 to 12 days (in the laboratory after 6 to 7 days). After 2–3-week feeding on the abaxial face of leaves larvae grew up and pupated in soil. Larvae of the 2nd generation damaged 5.6 cm^2 leaves of *S. fragilis* in July, i.e. nearly 2 times more than larvae of the 1st generation in May and June. In August and September, the nutritional value of food further decreases and mean daily temperatures also decrease. An average leaf area damaged by larvae was rather high, viz in August 3.8 and in September 3.5 cm^2 (Table 14). Increased toughness of leaves demonstrated in the increased wear of mandibles

Table 19. Mean week area of leaves of *S. fragilis* damaged by imagoes of the 2nd and 3rd generations of *P. vitellinae* including the mean week number of frass pellets and laid eggs. Laboratory rearings, 2005

Week	2nd generation						3rd generation					
	1♂/1♀			1♀			1 ♂/3 ♀♀			1 ♂/3 ♀♀		
	(cm²)	frass pellets	eggs	(cm²)	frass pellets	eggs	(cm²)	frass pellets	eggs	(cm²)	frass pellets	eggs
1st	2.5	274	0	2.8	209	0	3.2	339	–	3.4	382	–
2nd	2.8	282	46	2.6	358	27	0.8	81	–	1.0	102	–
3rd	1.7	172	39	3.5	460	46	–	–	–	–	–	–
4th	1.2	154	36	2.9	317	39	–	–	–	–	–	–
5th	0	0	0	2.7	345	39	–	–	–	–	–	–
6th	–	–	–	2.6	310	32	–	–	–	–	–	–
7th	–	–	–	3.4	382	24	–	–	–	–	–	–
8th	–	–	–	2.9	348	15	–	–	–	–	–	–
9th	–	–	–	2.7	334	26	–	–	–	–	–	–
10th	–	–	–	2.4	303	9	–	–	–	–	–	–
11th	–	–	–	1.3	201	–	–	–	–	–	–	–
12th	–	–	–	0.7	96	3	–	–	–	–	–	–
13th	–	–	–	0.1	10	–	–	–	–	–	–	–
Total	8.2	882	121	30.6	3,673	260	4.0	420	–	4.4	484	–
Non-laid (number)			4			18			–			–
Period of rearing	3 August– 2 September			19 August– 15 November			15 September– 23 September			23 September– 4 October		

probable participated in the decrease of the average damaged area (as against July).

Under natural conditions of southern and central Moravia, beetles of the 2nd generation occur on trees usually from mid-August till the beginning of October. For a period of 10 to 14 days, they feed on leaves (or buds and fine bark) in apical parts of shoots. These beetles do not mate in nature and after the termination of feeding they search for suitable winter shelters. Under laboratory conditions, the chrysomelid created 3 generations per year the 2nd and particularly the 3rd generation being not complete (Table 6). Beetles of the 2nd generation sexually matured during feeding, repeatedly copulated and females laid eggs. During about 1.5 months, females laid about 190 eggs and after oviposition died within several days (Tables 5 and 19). Only beetles of the 3rd generation left for wintering places after 8- to 11-day feeding (without a previous copulation) (Table 20). Average leaf area damaged by the beetles (4.2 cm²) was 6.8 times smaller as against last year's beetles from nature and compared to beetles of the 1st and 2nd generations from rearings 4.4 times smaller.

Results of the study show that generation conditions of *P. vitellinae* are rather complicated. In consequence of the long period of reproduction and relatively fast preimaginal development all developmental stages occur from June till the beginning of September. Under usual climatic-meteorological conditions 2 generations develop in the CR. The first generation is complete (i.e. a generation established by last year's imagoes after hibernation), the 2nd generation is only partial (i.e. a generation established by imagoes of the 1st generation).

Also Henschel (1895), Schnaider (1957) and Kadłubowski and Czalej (1962) rank the beetle among bivoltine species. According to Živojinovič (1948), Wagner and Ortmann (1959), Schnaider (1972), Vasiljev et al. (1974), Maisner (1974), etc. the chrysomelid has 2 to 3 generations per year. A sympatric and biologically related species *P. vulgatissima* developing mainly on *S. viminalis* is obligatorily univoltine in Great Britain (Kendall, Wiltshire 1998).

Natural enemies

Extreme weather during of winter and at the beginning of the growing season is the most efficient natural regulator of the abundance of *P. vitellinae.* Eggs and larvae of the chrysomelid are killed by bugs *Rhagognathus punctatus* (L.) (Pentatomidae) and *Anthocoris nemorum* L. (Anthocoridae). Mycoses of prepupae, pupae and imagoes are often caused by

Table 20. Mean period of the life of male and female imagoes of *P. vitellinae* reared in the laboratory during June to September (days). The mean period of life of imagoes with a spring/summer diapause is given in parentheses. The table also gives the mean number of laid eggs and mean damaged leaf area. Laboratory rearings on *S. fragilis*, 1998–2005

Sex/Number	June	July	August	September
Males	36	40	44	300 (323)
Females	30	38	48	293 (330)
Mean	33	39	46	297 (326)
Number of eggs	176	45	138	0
Damaged area (cm^2)	18.4	15.6	16.4	4.8

Beauveria bassiana (Bals.) (det. D. Novotný, Brno). For example *Syrphus vitripennis* Meig. (Maisner 1974) and *Parasyrphus nigritarsis* (Zett.) (Köpf et al. 1997; Rank et al. 1998) belong to predators of larvae and eggs. According to Augustin and Lévieux (1993) *Meigenia mutabilis* (Fall.) (Tachinidae) and allegedly also *Schizonotus latus* (Walk.) and *S. sieboldi* (Ratz.) (Pteromalidae) parasitize in larvae. Imagoes of the chrysomelid are killed by birds (Aves) (Lundvall et al. 1998), spiders (Aranea), etc.

Harmfulness

P. vitellinae damages mainly osier plantations, poplar nurseries, young willow and poplar plantations and shelter belts (Maisner 1974). Gradation is rather frequent and during a mass outbreak, it threatens the existence of young (particularly 1-year-old) plantations (Escherich 1923). According to Schnaider (1957) parts of plantations adjacent to forest stands are most damaged. Imagoes feed on newly unfolded leaves in tops of growing shoot. Larvae jointly skeletonize leaves in lower parts of shoots and during feeding they proceed from below upwards. Thus, often normally foliated shoots rank among preferentially damaged apical and proximal parts of shoots. Heavily damaged leaves look like leaves attacked by a rust. Leaves gradually dry, brown and grow black. During gradations which usually do not take longer than 2 years all leaves are often damaged. Under conditions of the lack of food beetles also feed on buds and fine bark at the end of shoots. The increment of trees due to the assimilatory area decrease or even total defoliation falls even stagnates. Destruction of buds and area damage to bark manifest themselves in the decline of distal parts of shoots. In the next year, shoots often branch thereby further technical devaluation occurs. The highest damage is caused by imagoes in the period of the development of leaves (Warchalowski 1973). According to the author, the feeding of larvae is not usually so harmful because it occurs in the period of the full foliage of shoots.

Based on our studies, last year's beetles of *P. vitellinae* damage about 29 cm^2 leaf area of *S. fragilis*, i.e. about 1.2 times more than beetles of *Plagiodera versicolora.* Larvae of the 1st generation destroy on average 4 cm^2 leaves, i.e. 1.4 times more than larvae of *P. versicolora*. Beetles after wintering as well as larvae of the 1st generation show the higher average consumption of food. Beetles of the 1st generation and larvae of the 2nd generation show a similar situation. According to our findings, however, the fecundity of *P. versicolora* is 1.5 times higher and the beetle has 3 to 4 generations per year. Under the same abundance of beetles of both species of chrysomelids appearing on host plants in spring the area of leaves of *S. fragilis* damaged by the whole population of *P. vitellinae* would be 1/3 lower than in *P. versicolora* (providing the same mortality). In spite of this simplified constatation it is necessary to consider *P. vitellinae* as an economically important physiogical and technical pest. Thus, it is necessary to control it particularly in case of threat to young forest plantations.

Protection and control

In the past, a number of protection and control measures was recommended against *P. vitellinae.* For example, Henschel (1895) regarded flooding of plantations as effective (of course, where it was technically practicable) as well as raking and burning fallen leaves and collection of beetles and larvae by sweep nets. Altum (1891) proposed to establish winter shelters for trapping beetles and subsequently to kill stiff beetles. Nüsslin and Rhumbler (1922) recommended controlled artificial floods and disposal of leaf litter including the collection of beetles and larvae. According to the authors, it is possible to shake off beetles to vessels (hung on a neck or carried on a chassis) and larvae can be killed by spraying or brushes. Rubner et al. (1942) mention shaking off beetles on underlaid umbrella-type shakers as well as effective using visceral insecticides (arsenates) to control the chrysomelid. According to Nejedlý

(1950), it is possible to kill *P. vitellinae* in osier plantations not only by a 2- or 3-week spring flood but also by their burning (in the period of early spring) or arsenate spraying.

After the World War 2, arsenates very dangerous for nature and man were changed by contact insecticides on the basis of chlorinated hydrocarbons. For example, Schnaider (1972) recommended DDT (in 5 to 10% concentration) or HCH spraying (in 1.2% concentration) at 10 kg/ha to control beetles. After the prohibition of chlorinated hydrocarbons particularly organophosphate preparations proved good (Attard 1979, etc.). Jodal (1985) used successfully Furadan G 10 (carbofuran) and Dimilin WP 25 (diflubenzuron) to control insect defoliators (including *P. vitellinae*). In the CR, it is possible to kill the chrysomelid by preparations given in the *List of permitted preparations for forest protection* which is issued and approved by the Ministry of Agriculture of the Czech Republic every second year.

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Received for publication March 20, 2006
Accepted after corrections April 20, 2006

Výskyt, vývoj a hospodářský význam *Phratora* (= *Phyllodecta*) *vitellinae* (L.) (Coleoptera, Chrysomelidae)

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ABSTRAKT: Práce shrnuje výsledky studia výskytu, vývoje a škodlivosti *Phratora* (= *Phyllodecta*) *vitellinae* (L.). Většina šetření byla vykonána v letech 1998 až 2005 v břehových a doprovodných porostech řeky Svitavy a Svratky na Brněnsku a v laboratoři. Imaga opouštějí hibernační úkryty koncem dubna, případně začátkem května. V zajetí žila na *Salix fragilis* kolem 2,5 měsíce, přičemž poškodila průměrně 28,6 cm^2 listové čepele a vykladla průměrně 293 vajíček. V nadměrně teplé vegetační sezoně 2005 imaga žila po hibernaci kolem 3,5 měsíce, avšak již po měsíci žíru upadala začátkem června do měsíční diapauzy. Před jejím nástupem poškodila průměrně 12,8 cm^2 (po diapauze 14,4 cm^2) listů a vykladla průměrně 389 vajíček (z toho 260 vajíček před diapauzou a 129 po ní). Larvy během 2 až 3 týdnů (v laboratoři během 12 až 13 dnů) poškodí kolem 4 cm^2 listů. Za 2 až 3 týdny (v laboratoři za 10 až 12 dnů) od skončení žíru se na dřevinách objevují mladí brouci. Imaga 1. generace se vyskytují od poloviny června do začátku října. Během asi 55denního života poškodila 19 cm^2 listů a vykladla průměrně 182 vajíček. Imaga 2. generace se vyskytují od poloviny srpna do konce vegetační sezony. Po desetidenním až 14denním žíru se (bez předchozí kopulace) uchylují do zimovišť. V laboratoři však tato imaga během 2 měsíců poškodila kolem 19 cm^2 listů a vykladla kolem 190 vajíček. Zimoviště vyhledávala imaga 3. generace, která před hibernací poškodila průměrně 4,2 cm^2 listů. *P. vitellinae* je v ČR obvykle bivoltinní, přičemž 2. generace je vždy neúplná.

Klíčová slova: Chrysomelidae; *Phratora* (= *Phyllodecta*) *vitellinae*; výskyt; hostitelské dřeviny; vývoj; generační poměry; škodlivost

Ve zřejmé souvislosti s klimaticko-meteorologickými anomáliemi a následným oslabením dřevin se v posledních desetiletích v ČR zvýšily populační hustoty lesnicky významných mandelinkovitých (Chrysomelidae). K aktivizaci došlo i u holarktické mandelinky *Phratora* (= *Phyllodecta*) *vitellinae* (L.), která je spolu se sympatrickou *P. vulgatissima* (L.) řazena k nejškodlivějším druhům mandelinek na dřevinách z čeledi Salicaceae. O jejím výskytu, biologii, škodlivosti a obraně existuje mnoho nejrůznějších (a někdy i protichůdných) údajů. Největší pozornost byla v poslední době věnována vlivu morfologie a chemického složení listů dřevin na trofickou selekci a vývoj mandelinky. Tato práce pojednává o málo známém výskytu, vývoji a škodlivosti imag a larev jednotlivých generací mandelinky. Většina šetření byla provedena v letech 1998 až 2005 v břehových a doprovodných porostech řeky Svitavy a Svratky na Brněnsku. Poznatky z přírody byly konfrontovány s rozsáhlými laboratorními šetřeními. Byly získány tyto nejdůležitější poznatky:

1. Podle terénních pozorování a laboratorních testů k nejoblíbenějším domácím hostitelským dřevinám *P. vitellinae* patří *Salix fragilis*, *S. nigricans* a *S.* × *rubens*. Velmi často je poškozována také *S. purpurea* a *Populus tremula* a dosti často *S. viminalis*, *S.* × *rubra* a *S.* cv. *Americana*. Zřídka až ojediněle (např. při přemnožení na primárních hostitelích) se vyskytuje např. na *S. caprea*, *S. alba*, *S. alba* var. *vitellina* a *S. cinerea*. Rezistentní jsou *S. triandra*, *P. alba*, některé klony *P. nigra* aj.
2. Na střední Moravě imaga opouštějí hibernační úkryty obvykle koncem dubna a začátkem května, na jižní Moravě obvykle ve třetí dekádě dubna. Poškozují rašící, případně čerstvě vyrašené listy (řidčeji pupeny a kůru) apikálních částí výhonků. Na *S. fragilis* imaga žila v zajetí průměrně 2,5 měsíce a poškodila průměrně 28,6 cm^2 listů. Ve velmi teplé vegetační sezoně 2005 imaga po 4 až 5 týdnech žíru upadala začátkem června do třítýdenní až pětitýdenní diapauzy. Tato imaga žila po přezimování průměrně 3,5 měsíce a poškodila průměrně 27,2 cm^2 listů (z toho 12,8 cm^2 před diapauzou a 14,4 cm^2 po ní). Průměrná spotřeba potravy samečků byla 2,4krát nižší než u samiček. Během žíru imaga defekovala průměrně 2 464 trusinek (o rozměrech 0,8 × 0,25 mm) a celkovém objemu 102,1 mm^3. Průměrný počet a celkový

objem trusinek z poškození o ploše 1 cm^2 se během vegetační doby průkazně zvyšoval. Tento nárůst souvisí s postupně se zhoršující nutriční hodnotou potravy.

3. Imaga přezimující generace se po týdenním žíru na listech poprvé páří a za další týden kladou první vajíčka. Samičky bez jarně-letní diapauzy kladly po dobu téměř dvou měsíců, samičky s diapauzou po dobu 2,5 měsíce. Vajíčka umísťují do osmičlenných až 20členných skupin na abaxiální stranu listové čepele, a to hlavně v proximálních částech výhonků. Opomíjení mladých listů při kladení omezuje potravní kompetici mezi imagy a larvami a snižuje mortalitu působenou hlavně hmyzími predátory a parazitoidy. V laboratoři samičky vykladly 43 % vajíček na abaxiální stranu listů, 12 % na adaxiální stranu listů a 45 % na stěny chovných nádob. Samičky (bez diapauzy) vykladly 191 až 546 (průměrně 293) vajíček, samičky (s diapauzou) 258 až 546 (průměrně 389) vajíček, z toho před diapauzou vykladly 67 % vajíček a po diapauze 33 % vajíček. Samčí imaga (bez diapauzy) žila po hibernaci průměrně 69 (samičí 57) dnů. Samčí imaga (s diapauzou) žila průměrně 93 (samičí 100) dnů. Samečci hynuli za jeden až dva týdny (samičky asi za týden) po skončení rozmnožování.
4. Vaječné larvy se líhnou za osm až 11 (v laboratoři za šest až sedm) dnů. Na rozdíl od *Plagiodera versicolora* a *Chrysomela populi* aj. larvy nikdy nekonzumují vaječné obaly. Cranium mají široké 0,39 až 0,46 mm a délku těla kolem 1,1 mm. V laboratoři na *S. fragilis* larvy po dobu 4,5 dne společně skeletovaly listy z abaxiální strany a dorůstaly délky kolem 2 mm. Průměrně poškodily 0,2 cm^2 listové čepele a defekovaly průměrně 109 trusinek o rozměrech kolem 0,18 × 0,07 mm.
5. Larvy 2. instaru mají cranium široké 0,59 až 0,69 mm a délku těla 1,5 až 3,8 mm. Na *S. fragilis* larvy čtyři dny společně skeletovaly listy z abaxiální strany. Průměrně poškodily 0,5 cm^2 listové čepele a defekovaly průměrně 168 trusinek o rozměrech kolem 0,36 × 0,13 mm.
6. Larvy třetího (tj. posledního) instaru mají cranium široké 0,86 až 1 mm a délku těla 3,4 až 6,2 mm. Na *S. fragilis* larvy pět dnů společně nebo v dílčích semknutých skupinách skeletovaly listy z abaxiální strany. Průměrně poškodily 2,1 cm^2 listové čepele a defekovaly průměrně 335 trusinek o rozměrech kolem 0,57 × 0,18 mm.
7. První generace larev se vyskytuje obvykle od 2. dekády května do poloviny srpna (v případě diapauzy imag až do poloviny září). Jejich vývoj od vylíhnutí z vajíček až do skončení žíru trvá dva až tři týdny (v laboratoři 12 až 13 dnů). Za tuto dobu larvy poškodí 2,8 až 5,6 (průměrně 4) cm^2 listů *S. fragilis*. Larvy žeroucí v květnu vyprodukují kolem 600 (v červenci kolem 1 000) trusinek. Bylo zjištěno, že se vzestupem početnosti larev ve skupinách mortalita larev průkazně klesá. Dorostlé larvy třetího instaru se kuklí v půdě v hloubce 1 až 4 cm. Předkukla trvá asi 4 (v laboratoři 2,5) dny, kukla asi 8 (v laboratoři 5,5) dnů. Asi po čtyřech (v laboratoři po 2,5) dnech imaga opouštějí kuklové kolébky. V přírodě se mladá imaga 1. generace objevují na dřevinách po dvou až třech týdnech (v laboratoři po 10 až 12 dnech) od skončení žíru larev.
8. *P. vitellinae* má na území ČR obvykle dvě generace, přičemž druhá generace je vždy neúplná. Na jižní a střední Moravě se imaga první generace vyskytují na dřevinách od poloviny června do konce vegetační doby. Asi po dvoutýdenním žíru (v laboratoři již po 10 až 12 dnech) začnou oplodněné samičky klást vajíčka 2. generace. Imaga 1. generace žila v zajetí průměrně 55 dnů a poškodila průměrně 18,8 cm^2 listů *S. fragilis* (samečci 2,5krát méně než samičky). Během 35denního období samičky vykladly 59 až 487 (průměrně 182) vajíček. Z poškození o ploše 1 cm^2 vyprodukovala průměrně 97 trusinek o celkovém objemu 3,8 mm^3. Průměrný počet a objem trusinek z 1 cm^2 se vlivem snížení nutriční hodnoty potravy od června do září zdvojnásobil, takže efektivita využívání potravy klesla na polovinu.
9. Imaga 2. generace se na dřevinách vyskytují obvykle od poloviny srpna do začátku října. Po dobu 10 až 14 dnů ožírají listy (příp. pupeny a jemnou kůru) v apikálních částech výhonků, načež vyhledávají vhodné hibernační úkryty. Tato imaga v laboratoři v průběhu žíru pohlavně dozrávala a opakovaně kopulovala. Během asi dvou měsíců poškodila kolem 19 cm^2 listů *S. fragilis* a za 1,5 měsíce vykladla kolem 190 vajíček. Imaga 3. generace setrvávala na výhoncích 8 až 11 dnů. Za tuto dobu poškodila průměrně 4,2 cm^2 listů a aniž by předtím kopulovala, odebírala se do zimovišť.
10. Imaga *P. vitellinae* ožírají listy (při pozdním rašení nebo při přemnožení také pupeny a kůru) apikálních částí výhonků a larvy skeletují listy v proximálních částech výhonků. Při masovém výskytu dochází k výraznému snížení asimilační plochy, případně až k totální defoliaci dřevin, což se projevuje snížením až zastavením přírůstu. Poškození pupenů a kůry může vést k nežádoucímu větvení výhonků a k odumírání jejich koncových částí. Nejhorší (často i mortální) dopady má poškození

zejména na jednoleté dřeviny. Bylo zjištěno, že imaga *P. vitellinae* poškodí průměrně 1,2krát (larvy 1,4krát) větší plochu než *Plagiodera versicolora*. Ta má však průměrně 1,5krát vyšší fekunditu a tři až čtyři generace v roce. Škodlivost celé populace *P. vitellinae* je proto (za předpokladu stejné mortality) nižší než u *P. versicolora*.

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