Occurrence, biology and harmfulness of *Galerucella lineola* (F.) (Coleoptera, Chrysomelidae) – Part 2. Larvae and this year's beetles

J. Urban

Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry Brno, Brno, Czech Republic

ABSTRACT: The second part of the paper deals with the development and harmfulness of larvae and maturation feeding of this year's beetles of *Galerucella lineola* (F.) before leaving for winter habitats. Embryogenesis takes on average 12 (in the laboratory 9) days. In the area of Žďár situated at a higher and colder location, larvae of the alder biological form occur on *Alnus glutinosa* and *A. incana* from June to August. In the warmer lowland area of Brno, larvae of the willow form occur on *Salix triandra*, *S. viminalis* and *S. caprea* from the 3rd decade of May to the beginning of August. In the laboratory, larvae of the alder form developed on average 16 days and larvae of the willow form 13 days. Larvae of the alder form damage on average 9.7 cm^2 leaves of *A. glutinosa* and larvae of the willow form 6.0 cm^2 leaves of *Salix caprea*. This year's imagoes occur in the area of Žďár on alders from mid-July to the end of October and during 3 weeks, they damage on average 16 cm^2 leaves of *A. glutinosa*. This year's imagoes occur on willows in the area of Brno from the end of June to the end of August. During 2 weeks, they damage on average 12 cm^2 leaves of *S. caprea*. The chrysomelid development is univoltine (in southern parts of Moravia partly bivoltine). The alder biological form of *G. lineola* produced 2 (the willow form even 4) incomplete generations in the laboratory. This year's imagoes damaged on average 36.6 cm^2 of *S. caprea* and laid 122 to 887 (on average 528) eggs. In the area of Brno, imagoes of the willow form were up to 65% parasitized by *Medina collaris* (Fall.) (Tachinidae).

Keywords: Chrysomelidae; *Galerucella lineola*; development of larvae; maturation feeding this year's beetles; generation conditions; natural enemies; harmfulness

Galerucella lineola (F.) is one of the most abundant and from the viewpoint of forestry also one of the most important species of the family Chrysomelidae. Taxonomically, it belongs to the subfamily of Galerucinae, which is represented by 30 species in the CR. It is known by the creation of two biological forms (alder and willow), which are morphologically identical, however, biologically different.

By its specified trophic link to host species the chrysomelid resembles *Lochmaea capreae* (L.), which creates also two biological forms (willow and alder). Willow forms of both species occur sometimes together on the same tree (e.g. in osier and bioenergy plantations). With respect to the considerably hygrophilous character of *G. lineola* and higher tolerance of *L. capreae* to different environment humidity, the coincidence of both species is, however, possible mainly on moist to waterlogged or flooded sites.

In 1995 to 2006, a marked increase was noted in the abundance of Chrysomelidae on forest trees at several places of Moravia. An increase in the population density of *G. lineola* was used to study its occurrence, biology and harmfulness in detail. The alder biological form was studied mainly in *Alnus glutinosa* Gaertn., Forest District Polnička (Žďár region) and the willow form in *Salix* spp. in riparian and accompanying stands of the Svitava River near

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Bílovice nad Svitavou (Brno region). Findings on the occurrence, development and harmfulness of both forms of the chrysomelid were obtained by field and laboratory studies. The paper was divided in two related parts. Part 1 deals with the hibernation of beetles, their host species, feeding, reproduction and natural enemies (Urban 2007). Part 2 of the paper deals particularly with the development and feeding of larvae and maturation feeding of young (this year's) imagoes before leaving for winter habitats.

G. lineola is a widely distributed Palaearctic species with the centre of occurrence in boreal parts of Eurasia. It tends to mass reproduction and, therefore, in entomological and forest protection literature, it is considered to be a pest. Ecologically, it is related to moist places mainly on banks of watercourses and reservoirs. In Moravia, parent (last year's) beetles fly in budding and newly unfolded leaves in the first half of May. In the CR, the alder biological form most often colonizes *A. glutinosa* and the willow form *S. viminalis* L., *S. caprea* L. and *S. triandra* L. During a 7 to 10-day maturation feeding on leaves of host trees, females sexually mature beginning to lay eggs. They place them into clutches of 3 to 20 (on average 14) on the abaxial face of leaves. During 2 to 2.5-month feeding, they damage on average 22.6 cm^2 leaves. The females reproduce for a period of 1.5 to 2 months and then die. Females of the willow biological form lay 457 to 791 (on average 612) eggs, females of the alder form up to 687 eggs (Urban 2007).

There are many simplified and sometimes also inaccurate data in literature on the development and harmfulness of *G. lineola* larvae. Eckstein (1897) writes that larvae live (similarly like larvae of *L. capreae*) on *S. caprea* where they skeletonize leaves. According to Nüsslin and Rhumbler (1922) and Escherich (1923) larvae hatch from eggs after 1 to 2 weeks skeletonizing leaves from the abaxial face. They damage leaves from the shoot top, unlike "blue chrysomelids" (*Phratora* spp. and *Plagiodera versicolora* [Laich.]) where the procedure of feeding is reverse. Ikonen et al. (2003) found that fully-grown larvae and pupae of alder populations always showed higher mean weight than larvae and pupae of willow populations regardless of whether they lived on the alder or on the willow.

Further details on the development of larvae were given by Kožančikov (1958). According to the author larvae develop on the abaxial face (rarely also on the adaxial face) of leaves. They skeletonize leaves either individually or in smaller groups. They complete their development in captivity on willows or poplars, although the author never found the chrysomelid on poplars. According to Kožančikov (1958) larvae can successfully develop on *Betula pubescens* Ehrh. or *A. glutinosa*, however, not on *A. incana* Moench. Newly hatched larvae of the willow biological form consumed only *S. nigricans* Sm. in rearings whereas larvae of the alder form preferred the alder at 71% and the willow at 29%. Thus, the willow form is specialized to willow nutrition whereas the alder form can consume both alder and willow leaves (although the alder much more). Starving larvae of the willow form consumed alder leaves reluctantly showing, however, high (80%) mortality. Larvae of the first generation of the willow form developing on *Populus tremula* L. showed high (80–90%) mortality and generally good growth. In the 2nd generation, the mortality of larvae declined to a half ranging within the limits 40–60% up to the 12th generation. However, not even after 12 generations did larvae fully adapt preferring willow to aspen (Kožančikov 1958).

Brovdij (1968, 1973) gives valuable findings on the preimaginal development of *G. lineola.* According to the author mainly smaller larvae are negatively phototropic because they occur on the abaxial face of leaves thereby fading from direct insolation. Particularly excessively dry weather affects unfavourably the development of larvae. Thus, up to 30% larvae can succumb. At low relative air humidity, larvae hardly moult and their development extends. Under warm and sunny weather, however, larvae (similarly like beetles) feed more intensively than under cold or windy weather. In the course of skeletonizing they do not damage the upper epidermis of the main or lateral veins of leaves. Maisner (1974) summarized findings on the occurrence, biology and harmfulness of the chrysomelid. According to him larvae skeletonize leaves at the beginning jointly. Later, they spread and damage leaves individually. In the absence of food they also can (similarly like beetles) damage buds and fine bark of shoots.

Food preference of *G. lineola* is in close relation to the preference of tree species at egg laying (Wirén, Larsson 1984; Seldal et al. 1994). The preference at egg laying reflects the suitability of leaves for the development of larvae. Larvae are relatively immobile and, therefore, they have only limited possibilities of food selection. They develop optimally on preferred species and full-grown larvae attain higher weight. In experiments carried out by Larsson et al. (1986), beetles preferred the leaves of *S.* × *dasyclados* Wimm. (= *S. cinerea* L. × *S. viminalis*) clones which grew at poor light and good nutrient supply when the leaves contained a low total concentration of phenolic substances. According to Tahvanainen et al. (1985) the chrysomelid colonizes preferentially species with the low content of salicin in leaves. However, it is evidently adapted to the high concentration of the glucoside salidroside in leaves of *S. triandra*. Considerable diversity of phenolglucosides in willow leaves is considered to be a selective force which controls (through the process of adaptation and specialization) the evolution and perhaps even the creation of the species.

For example, KENDALL et al. (1996) mentioned repellent and inhibitory (according to KOLEHMAINEN et al. 1995 also stimulation) effects of phenolglucosides in leaves of willows. The development of the chrysomelid can also be negatively affected by proteinase inhibitors the formation of which is induced by injury in leaves of *A. incana* (SELDAL et al. 1994). Through the damage to host trees the quality of food gets worse (e.g. the content of nutrients, tannins and phenolglucosides is changed) (RAUPP, SADOF 1991).

Larvae of *G. lineola* can live on a broader spectrum of willows than e.g. larvae of *Phratora vitellinae* (L.). They have no dorsal glands excreting defensive secretions, the precursor of which are phenolic glucosides (e.g. salicin) contained in leaves. According to DENNO et al. (1990) larvae develop well on *S. viminalis* (poor in salicylates) and *S. fragilis* (rich in salicylates) and poorly on *S.* × *dasyclados* (rich in other phenolic compounds than salicylates). HÄGGSTRÖM and LARSSON (1995), HÄGGSTRÖM (1997), HÄGGSTRÖM and ANDERSON (1997) tested the mortality of larvae on trophically optimum *S. viminalis* and suboptimum *S.* × *dasyclados* and their hybrids. On *S. viminalis*, larvae developed more quickly showing lower mortality and large size than on *S.* × *dasyclados*. The suitability of hybrids as against the parent tree species was intermediary. Studies of these authors proved a hypothesis that insects developed slowly on unsuitable plants. Thus, larvae are subject to the effect of natural enemies for a long time. Particularly eggs and larvae of the first instar are exposed to the pressure of opponents (HÖGLUND et al. 1999).

Easily vulnerable neonatal larvae of *G. lineola* show a trend to look for various shelters on *S. viminalis* (e.g. rolled down leaf margins, terminal buds, large veins and galls) (LARSSON et al. 1997). The shelters provide a suitable microclimate (above all higher moisture) and partly also protection from nonspecific predators. Larvae develop better in the shelters and their mortality is also lower. Leaves of *S. bicolor* Willd. (= *S. phylicifolia* L.) from wetlands are of lower quality for the nutrition of *G. lineola* as compared to leaves of the willow growing at dry places (SIPURA et al. 2002).

Nevertheless, young larvae (particularly larvae of the 1st instar) do not thrive well at dry sites in spite of the higher quality of food. On the other hand, their development is optimal at moist sites. In laboratory rearings of SIPURA and TAHVANAINEN (2000), imagoes preferred shade leaves to leaves of trees from open locations. Larvae on shade leaves also developed better. However, the situation was quite different in nature. Therefore, the authors assumed that the outdoor environment (in spite of the lower quality of sunlit leaves) was more favourable for the occurrence and development of the chrysomelid.

BJÖRKMAN et al. (2000) studied the effects of the quality of *S. cinerea* leaves (assessed according to the length of shoots) on the development of larvae, fecundity of females and the density of unspecialized

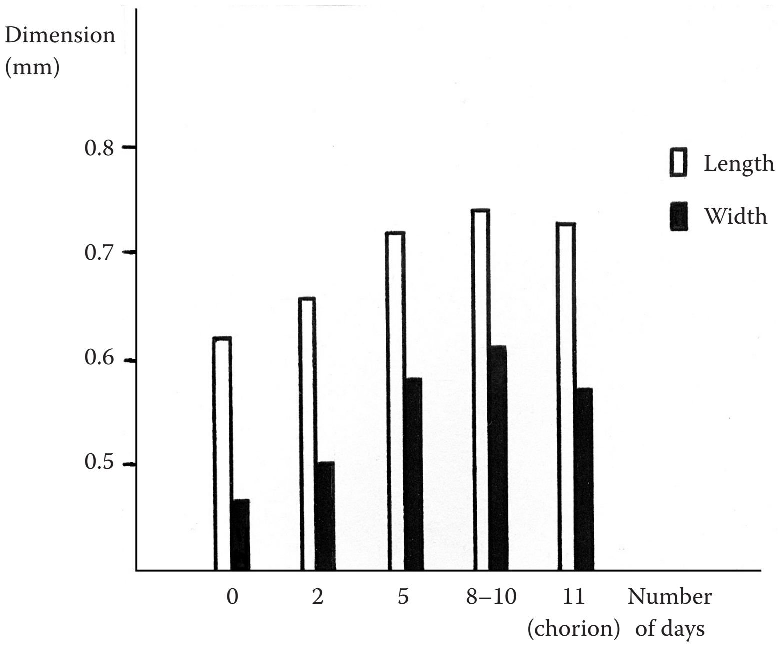

Fig. 1. Egg dimensions of the willow biological form of *Galerucella lineola* during embryonal development. Laboratory examination, 2006

predators. In the stand part with the pest gradation (where the length of shoots was 72% higher), larvae developed in the same way and females were of the same fecundity as in the stand part free of the pest gradation. However, in an area free of gradation, the density of non-specialized predators was significantly higher.

Bogacheva (1998) studied the adaptation of Chrysomelidae to climatic unfavourable conditions in the area of the lower Ob River. At the increase of temperature from 10 to 20°C, the growth and development of larvae accelerate nearly 3.8 times. With decreasing temperature the period of the growth of larvae extends substantially less than the period of moulting. The period of moulting of the larvae of Galerucinae is about 2 to 5 times longer than that of Chrysomelinae (Bogacheva 1998). Veteli et al. (2002) dealt with the effects of supposed global climatic changes (increased temperature and CO_2 concentration) on the quality and quantity of the aboveground biomass of willows (and the development of larvae).

MATERIAL AND METHODS

The alder biological form of *G. lineola* was studied in 3 to 20-years-old stands of *A. glutinosa* and *A. incana* (at an altitude of about 650 m), Polnička Forest District (Forest Enterprise of Dr. R. Kinský, Žďár nad Sázavou) in 1995 to 1998. The willow form was studied on *S. triandra*, *S. viminalis* and *S. caprea* shrubs of the same age in riparian and accompanying stands of the Svitava River (at an altitude of about 235 m) in the stretch between Bílovice nad Svitavou and Adamov (former Brno-venkov District) in 1999–2006. Moreover, the chrysomelid was also studied in laboratory rearings on alder and willow leaves during the growing season. Particular instars of larvae were determined according to the micrometrically measured width of the cranium. A leaf area damaged by larvae and this year's imagoes was measured with a planimeter. Further details on the studied localities and field and laboratory operations are given in Part 1 of the paper (Urban 2007).

RESULTS AND DISCUSSION

Embryonal development

Under natural conditions of Moravia, eggs of *G. lineola* occur usually from mid-May to the end of July or beginning of August. At this time, the light phase of the day extends and mean daily temperatures usually increase. The increase in temperature is closely related to the relative atmospheric humidity, which is of great importance for the embryonal development. Relatively high demands of the chrysomelid on moisture are reflected in the preferential colonization of shrubby species growing on waterlogged or flooded sites close to waters. Through evapotranspiration, the relative humidity increases in the ground layer. This humidity stimulates the development of embryos and larvae (particularly of the 1st instar). The immediate contact of eggs with the leaf parenchyma also shows positive effects on the embryonal development and hatching of larvae. As mentioned in Part 1 (Urban 2007), females lay eggs usually on small spots with removed epidermis. Eggs obtain water from leaf tissues and thus, their dimensions gradually increase during the embryonal development. For example, the mean length of eggs of the willow biological form increases by 19.4% and width by 29.8% (Fig. 1).

Under favourable conditions, the embryonal development takes 12 to 15 days (Brovdij 1973). In Scandinavia, larvae hatch after 2 to 3 weeks (Häggström, Larsson 1995) and in Iran after 12 to 16 days (Sadeghi et al. 2004). At the studied localities in Mora-

Table 1. Development of the alder biological form of *G. lineola* (from egg laying to the occurrence of imagoes) on *Alnus incana* and *A. glutinosa*. Mean damaged area of leaves is given in the numerator, mean period of development in the denominator. Laboratory examination, 1996 to 1998

Host species	Date of egg laying	Embryonal development (days)	Leaf area (cm^2)/period of development (days)				Development in soil (days)
			1st instar	2nd instar	3rd instar	total	
A. incana	17 May 1996	8	1.1/7	2.6/6	7.9/8	11.6/21	11.0
	20 May 1997	9	0.9/5.5	2.8/5	9.7/6.5	13.4/17	10.0
Mean		8.5	1.0/6.2	2.7/5.5	8.8/7.2	12.5/19	10.5
A. glutinosa	18 May 1998	9	0.4/6	1.2/5	7.5/7	9.1/18	14.0
	28 May 1998	9	0.4/5	1.5/4	9.3/7	11.2/16	14.0
	14 July 1998	9	0.4/5	1.0/4	7.4/6	8.8/15	12.0
Mean		9	0.4/5.3	1.2/4.3	8.1/6.7	9.7/16.3	13.3
Total mean		8.8	0.7/5.7	2.0/4.9	8.4/6.9	11.1/17.5	11.9

Table 2. Development of the willow biological form of *G. lineola* (from egg laying to the occurrence of imagoes) on *Salix fragilis* and *S. caprea*. Mean damaged area of leaves is given in the numerator, mean period of development in the denominator. Laboratory examination, 1998, 1999 and 2006

Host species	Date of egg laying	Embryonal development (days)	Leaf area (cm^2)/period of development (days)				Development in soil (days)	Generation
			1st instar	2nd instar	3rd instar	total		
S. fragilis	18 May 1998	10	0.2/4.5	0.5/4	2.4/6	3.1/14.5	15	1st
	13 May 1999	10	0.2/5	0.6/4	3.4/6	4.2/15	13	
	15 May 1999	10	0.2/5	0.5/4	3.0/6	3.7/15	13	
	20 May 1999	10	0.2/4	0.5/3.5	3.1/4.5	3.8/12	15	
	21 May 1999	10	0.2/4	0.6/3.5	3.7/4.5	4.5/12	15	
	23 May 1999	9	0.2/4.5	0.6/3.5	3.8/5	4.6/13	15	
	Mean	(9.8)	–	–	–	(4.0/13.6)	(14.3)	
	30 June 1999	8	0.2/4	0.6/3.5	3.0/4	3.8/11.5	14	2nd
	3 July 1999	8	0.2/4	0.6/3.5	2.6/4.5	3.4/12	12	
	7 July 1999	8	0.2/4.5	0.6/3.5	2.5/5	3.3/13	12	
	10 July 1999	8	0.2/4	0.6/3.5	3.4/4.5	4.2/12	13	
	11 July 1999	8	0.3/4	0.7/3.5	3.8/4.5	4.8/12	12	
	13 July 1999	8	0.2/4	0.7/3.5	3.4/4.5	4.3/12	12	
	Mean	(8)	–	–	–	(4.0/12.1)	(12.5)	
	14 August 1999	9	0.3/4.5	0.8/4	4.0/5.5	5.1/14	15	3rd
	17 August 1999	9	0.2/4.5	0.6/4	3.6/5.5	4.4/14	15	
	21 August 1999	9	0.2/5	0.6/4.5	3.5/6	4.3/15.5	14	
	Mean	(9)	–	–	–	(4.6/14.5)	(14.7)	
	23 October 1999	10	?	?	?	?	?	4th
	Total (mean)	(8.9)	(0.2/4.4)	(0.6/3.7)	(3.3/5.1)	(4.1/13.2)	(13.7)	1st–4rd
	19 May 2006	9	0.2/4.5	0.6/3.5	3.4/5	4.2/13	11	1st
	24 June 2006	8	0.2/3.5	0.7/3	3.2/4.5	4.2/11	10	2nd
	11 August 2006	9	0.2/4.5	0.6/4	3.1/6	3.9/14.5	14	3rd
	Mean	(8.7)	(0.2/4.2)	(0.6/3.5)	(3.3/5.1)	(4.1/12.8)	(11.7)	1st–3rd
S. caprea	13 August 2006	9	0.3/5.5	0.9/4.5	4.8/6	6.0/16	14	3rd
Total mean		(8.9)	(0.2/4.7)	(0.7/3.9)	(3.8/5.4)	(4.7/14)	(13.1)	1st–3rd

via, larvae hatch usually after 10 to 14 (on average 12) days. Under laboratory conditions, the embryonal development lasted 7 to 11 (on average 9) days (Tables 1 and 2). It follows that embryogenesis shortens with the increasing environment temperature. Egg larvae leave egg envelopes through irregular (as a rule lateral) 0.34 × 0.24 mm holes (Fig. 2). Larvae never consume egg envelopes after eclosion (unlike larvae of *Plagiodera versicolora* [Laich.], *Chrysomela populi* [L.] etc.). Newly hatched larvae darken during about 3 hours and begin to ingest during several other hours (when their body integuments get hard).

Development of larvae

Free-living larvae of *G. lineola* occur on the abaxial face of leaves. Only older larvae occur sporadically also on the adaxial face of leaves under cloudy weather. Younger larvae live usually in smaller groups, older larvae spread on leaves and live mostly separately. At a colder locality in the Žďár area, larvae occur on trees from the beginning of June to the end of August. At a climatically more favourable locality in the Brno area, larvae occur usually from the 3rd decade of May to the beginning of August.

Literature data on the period of the occurrence of larvae differ. In Bavaria (nearby the frontier with the CR), larvae were found on *A. glutinosa* (rarely on *A. incana*), namely from 17 June to 25 September (most abundantly in mid-July) (Gharadjedaghi 1997). In Sweden, larvae feed from May to the beginning of August (Häggström, Larsson 1995; Larsson et al. 1997). In Spain, larvae begin to hatch at the beginning of June and live about one month on the abaxial face of leaves (Vicente et al. 1998). In Iran, larvae of the 1st instar occur already in the

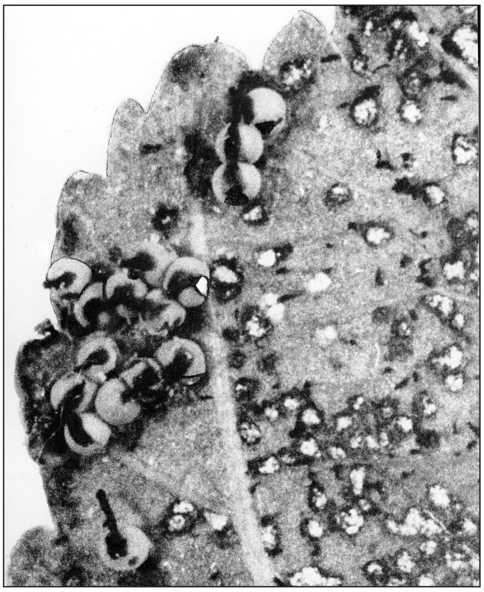

Fig. 2. Abaxial face of leaves of *A. glutinosa* damaged by larvae of the 1st instar of *G. lineola* (including abandoned egg envelopes). Laboratory rearing, 11 June 1998

2nd week of May (Sadeghi et al. 2004). The first instar takes there 5 to 6 days, the 2nd instar 5.5 to 7 days and the 3rd instar 7 to 10 days. In Ukraine, the first larvae hatch already in mid-May and their development takes 27 to 30 days (Brovdij 1973).

Larvae of the 1st instar of the alder biological form of *G. lineola* live in the Žďár area on average 9 days, in the laboratory 5.7 days. Within the period, they damage on average 0.4 cm^2 leaves of *A. glutinosa* and 1.0 cm^2 leaves of *A. incana* (Table 1). Larvae of the 1st instar of the willow form live in the Brno area on average 7 days, in the laboratory 4.5 days. Within the period, they damage on average 0.2 cm^2 leaves of *S. fragilis* and defecate on average 231 frass pellets (Tables 2 and 3). Frass pellets are black, on average 0.2 mm long and 0.04 mm wide (Table 4). Holes reach the upper epidermis which remains always undamaged. Leaf veins including vein anastomoses remain also intact. Around the venation, larvae usually leave remnants of intact leaf tissues which often reach greater diameters than feeding marks. The cranium of larvae of the 1st instar of the alder biological form is 0.28 to 0.39 (on average 0.33) mm wide. The cranium of larvae of the willow form is 0.27 to 0.36 (on average 0.31) mm wide (Fig. 5).

Larvae of the 2nd instar of the alder biological form develop in the area of Žďár on average 8 days, in the laboratory 5 days. They damage on average 1.2 cm^2 leaves of *A. glutinosa* and 2.7 cm^2 of *A. incana* (Table 1). Larvae of the 2nd instar of the willow form develop in the Brno area on average 6 days, in the laboratory 3.5 days. Within the period, they damage on average 0.65 cm^2 leaves of *S. fragilis* and defecate on average 231 frass pellets of the mean length of 0.5 mm and width 0.09 mm (Tables 2, 3 and 4). Larvae skeletonize, usually separately. They bite irregular feeding marks of a diameter about 0.8 mm into the leaf blade (Figs. 3 and 6). They do not damage lateral veins and usually even vein anastomoses. They leave only minimum remains of intact tissues along veins and anastomoses. The cranium of larvae of the 2nd instar of the alder biological form is 0.43 to 0.61 (on average 0.52) mm wide. The cranium of larvae of the willow form is 0.39 to 0.57 (on average 0.49) mm wide (Fig. 5). Full-grown larvae of the 2nd instar stop to ingest and prepare for moulting on average for a period of 6 hours. The actual ecdysis takes only 10 to 15 minutes in the laboratory. Newly hatched yellowish larvae of the 3rd instar remain in exuviae by their tail-end for a period of about 2.5 hours. About 3 hours after moulting, larvae are almost black. They begin to ingest 8 to 10 hours after moulting. The whole process of moulting takes 14 to 16 hours, in nature about 1 day.

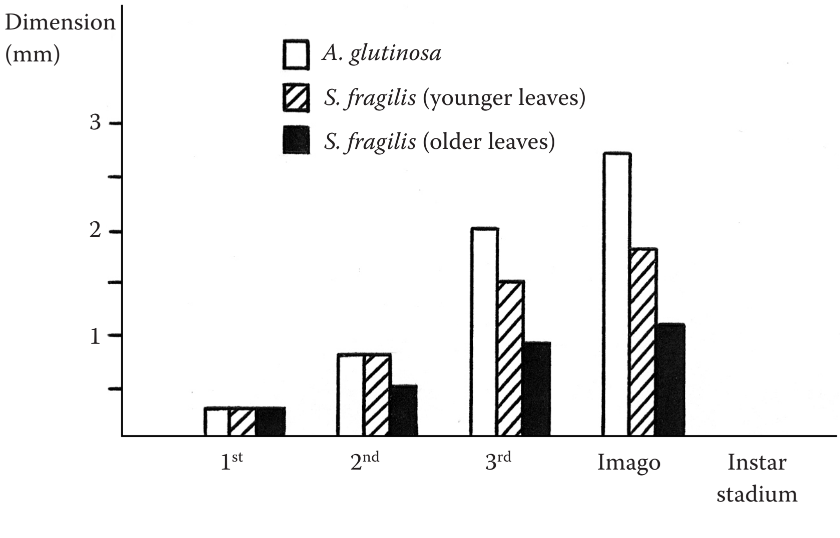

Fig. 3. Mean dimensions of feeding marks of larvae of the 1st to the 3rd instar and imagoes of the alder biological form of *G. lineola* on leaves of *A. glutinosa* and of the willow biological form of *G. lineola* on leaves of *S. fragilis*

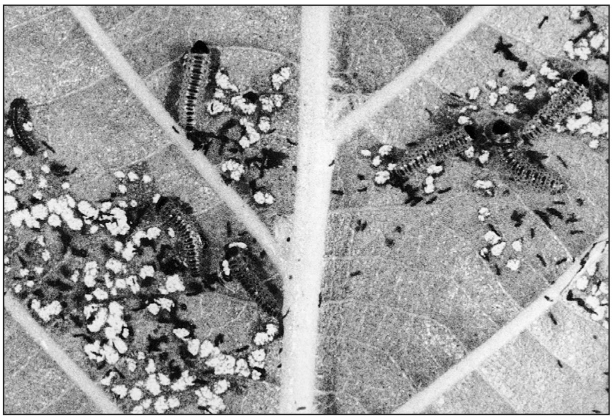

Fig. 4. Larvae of the 1st instar of *G. lineola* at feeding on the abaxial face of leaves of *A. glutinosa*. Laboratory rearing, 8 June 1996

Larvae of the last instar (3rd) of the alder biological form develop in the Žďár area on average 11 days, in the laboratory 7 days. Within the period, they damage on average 8.1 cm^2 leaves of *A. glutinosa* and 8.8 cm^2 leaves of *A. incana* (Table 1). Larvae of the 3rd instar of the willow form develop in the Brno area on average 8 days, in the laboratory 5 days. On average, they damage 3.2 cm^2 leaves of *S. fragilis* and defecate on average 595 frass pellets of the mean length of 0.8 mm and width 0.17 mm (Tables 2, 3 and 4). As a rule, they skeletonize leaves and sometimes also punch the youngest leaves. They damage leaves separately, often including fibrous anastomoses and fine ends of lateral veins. Feeding marks of larvae of the 3rd instar of the alder biological form are on average larger (about 2 mm) than feeding marks of larvae of the willow form (about 1.5 mm) (Figs. 3, 6 and 7). The cranium of larvae of the last instar of the alder biological form is 0.68 to 0.93 wide (on average 0.82) mm. The cranium of larvae of the willow form is 0.68 to 0.86 (on average 0.77) mm wide (Fig. 5).

Larvae of all three instars of the alder biological form of *G. lineola* developed in the area of Žďár on average 4 weeks (in the laboratory on *A. glutinosa* 16.3 days and on *A. incana* 19 days) (Table 1). Larvae of the willow form developed in the Brno area on average 3 weeks (in the laboratory 13 days) (Table 2). Larvae of the alder form damaged on average 9.7 cm^2 leaves of *A. glutinosa* and 12.5 cm^2 leaves of *A. incana* (Table 1). Larvae of the willow form damaged on average 4.0 cm^2 *S. fragilis* and 6.0 cm^2 *S. caprea.* On *S. fragilis*, they defecated on average 1,057 frass pellets of a total volume of 11.8 mm^3. Larvae of the 1st instar damaged 5%, larvae of the 2nd instar 17% and larvae of the 3rd instar 78% of the total damaged area (Table 3). Fig. 8 demonstrates the average area of leaves damaged by larvae of the 1st to the 3rd instar on *A. glutinosa*, *A. incana*, *S. fragilis* and *S. caprea.* According to Kožančikov (1958), larvae of the alder biological form attain higher mean size than larvae of the willow form. Larvae of the alder biological form develop in nature and laboratory 1.3 to 1.5 times longer than larvae of the willow form. The average leaf area damaged by larvae of the alder biological form is also 1.6 to 3.1 times larger as compared with the average leaf area damaged by larvae of the willow biological form. *A. glutinosa* is trophically much more suitable for the alder

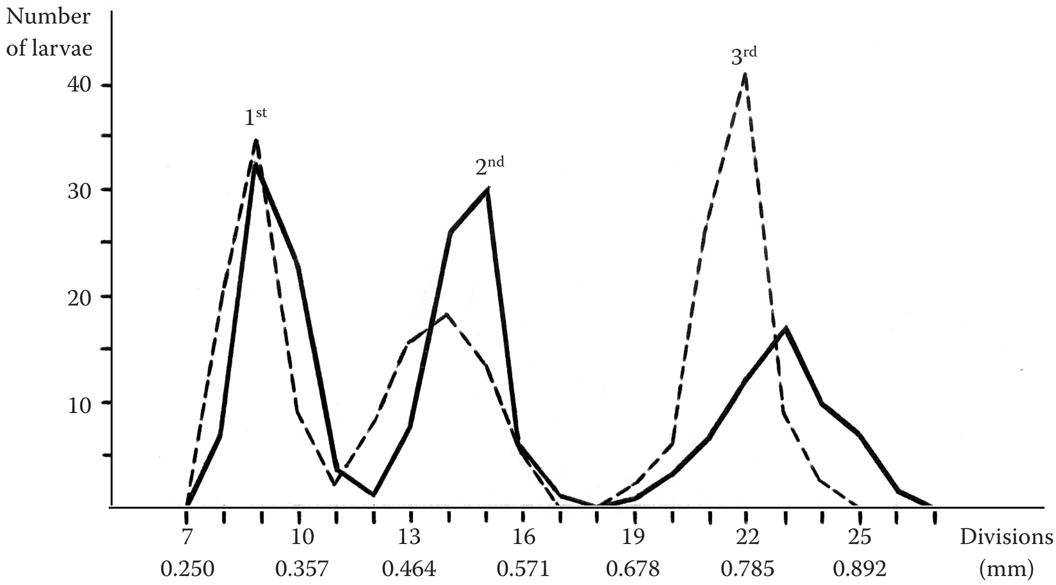

Fig. 5. The width of a cranium of larvae of the 1st to the 3rd instar of the alder biological form (dash line) and of the willow biological form of *G. lineola* (solid line). Mean width of the cranium of larvae of the 1st instar of the alder form is 0.33 mm and that of the willow form 0.31 mm. Mean width of the cranium of larvae of the 2nd instar of the alder form is 0.52 mm and that of the willow form 0.49 mm. Mean width of the cranium of larvae of the 3rd instar of the alder form is 0.82 mm and that of the willow form 0.77 mm (1 division = 0.0357 mm). Laboratory examination, 1996 to 2006

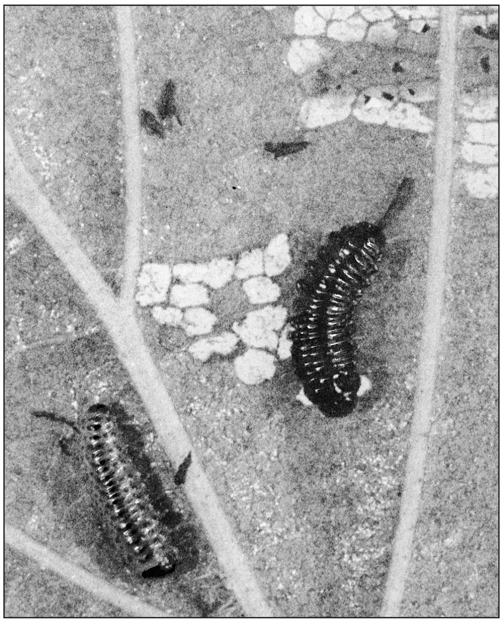

Fig. 6. Larvae of the 2nd and 3rd instars of *G. lineola* at feeding on the abaxial face of leaves of *A. glutinosa*. Laboratory rearing, 20 June 1998

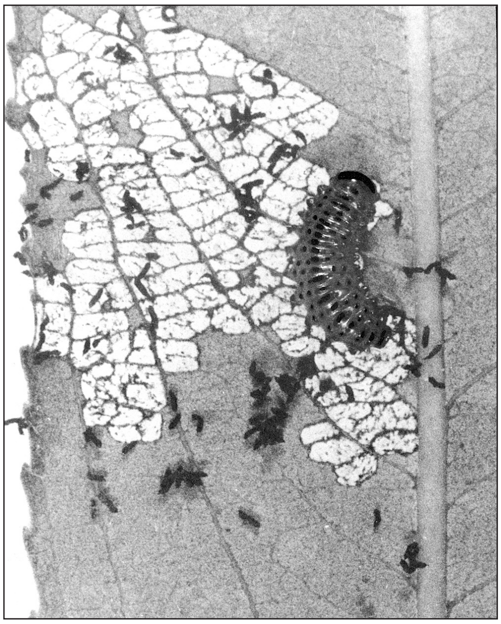

Fig. 7. Growing up larva of the 3rd instar of *G. lineola* at feeding on the abaxial face of leaves of *S. fragilis*. Laboratory rearing, 8 June 1998

biological form than *A. incana*. Larvae develop on *A. glutinosa* on average for a shorter time, show lower mortality and damage on average a smaller area of leaves than on *A. incana*.

Pupation of larvae and hatching of imagoes

Larvae of the 3rd instar of the alder biological form of *G. lineola* grow up in the area of Žďár usually from the end of June to the end of August. Then, they leave their host trees and come down to the ground along the tree stem (according to some data they fall to the soil surface). In litter or in the surface layer of soil (at a depth of 3 to 4 cm), they make a pupal chamber with smooth walls ("earth cocoon"). According to Brovdij (1973) larvae pupate in chambers placed at a depth of about 5 cm (maximally 8 cm) and according to Sadeghi et al. (2004) at a depth of 5 to 10 cm at the stem foot or near the tree base.

In the pupal chamber, larvae prepare for pupation for about 4 days (in the laboratory on average 3 days). The actual stage of pupa takes about 8 days (in the laboratory on average 7 days). Newly hatched (i.e. this year's) imagoes remain in chambers for about

Table 3. The area of leaves of *S. fragilis* and *S. caprea* damaged by larvae of the 1st and 2nd generations of *G. lineola*. The number and volume of frass pellets produced by larvae on *S. fragilis*. Laboratory examination, 2006

Generation Host species (development)	Instar	Mean damaged leaf area		Mean number of frass pellets		Volume of one frass pellet (mm^3)	Volume of frass pellets	
		(cm^2)	(%)	(number)	(%)		(mm^3)	(%)
1st *S. fragilis* (27 May–2 June)	1st	0.2	4.7	228	20.1	0.00025	0.057	0.4
	2nd	0.7	16.3	223	19.7	0.00392	0.874	6.6
	3rd	3.4	79.0	681	60.2	0.01815	12.360	93.0
	total	4.3	100.0	1,132	100.0	–	13.291	100.0
2nd *S. fragilis* (2 July–16 July)	1st	0.2	5.3	234	23.8	0.00025	0.059	0.6
	2nd	0.7	18.4	240	24.4	0.00392	0.941	9.2
	3rd	2.9	76.3	509	51.8	0.01815	9.238	90.2
	total	3.8	100.0	983	100.0	–	10.248	100.0
2nd *S. caprea* (22 August–9 September)	1st	0.3	5.0	?	?	?	?	?
	2nd	0.9	15.0	?	?	?	?	?
	3rd	4.8	80.0	?	?	?	?	?
	total	6.0	100.0	?	?	?	?	?

Table 4. Mean length/width of frass pellets of imagoes and larvae of the 1st–3rd instars of the alder biological form of *G. lineola* on *A. glutinosa* and of the willow biological form on *S. fragilis* (mm). Mean volume of frass pellets (mm³). Laboratory examination, 1995 to 2006

Stage Growth degree		Biological form alder	Biological form willow	Ratio of the volume of frass pellets
Imago	length/width	1.00/0.19	0.84/0.11	3.5:1
	volume	0.0283	0.0080	
1st instar	length/width	0.28/0.06	0.20/0.04	2.7:1
	volume	0.0008	0.0003	
2nd instar	length/width	0.74/0.12	0.50/0.09	2.6:1
	volume	0.0084	0.0032	
3rd instar	length/width	1.00/0.23	0.80/0.17	2.3:1
	volume	0.0415	0.0181	

3.5 days (in the laboratory on average 3 days). In nature, the chrysomelid occurs in a chamber 13 to 18 (on average 15.5) days, in the laboratory 10 to 16 (on average 13) days (Tables 1 and 2). The total period of the chrysomelid development in soil is affected by the soil temperature. At lower mean temperatures in May 1996, the chrysomelid developed in soil on average 14 days, at higher temperatures in June and July only 12.5 days (Table 2). Young beetles then leave the chambers and appear on host trees. According to Maisner (1974) the stage of a pupa takes 6 to 7 days, according to Sadeghi et al. (2004) 7 to 9 days.

Maturation feeding of this year's imagoes

In the area of Žďár, young (this year's) imagoes of the alder biological form of *G. lineola* occur on trees usually from mid-July to the end of October. Under favourable weather (e.g. in 1995), imagoes were found on alder trees even at the beginning of November (Table 5). In the Brno area, this year's imagoes of the willow biological form occur on trees usually from the end of June (i.e. about 2 weeks earlier) to the end of August (exceptionally till the beginning of September). In Bavaria, this year's imagoes occur on alders from mid-July to mid-October (maximum abundance at the end of August and at the beginning of September) (Gharadjedaghi 1997). In the Baltic region, imagoes hatch from mid-July to the beginning of September (Kožančikov 1958). In Iran, according to Sadeghi et al. (2004) imagoes occur in the open from the beginning of July to mid-August. Imagoes concentrate on terminal parts of shoots intensively punching young growing up and grown-up leaves. In osier plantations in Moravia, this year's imagoes living on willows (particularly on *S. viminalis*) often hide in leaf rolls of caterpillars of *Earias clorana* (L.) (Nolidae), *Acleris hastiana* (L.), *Archips rosanus* (L.),

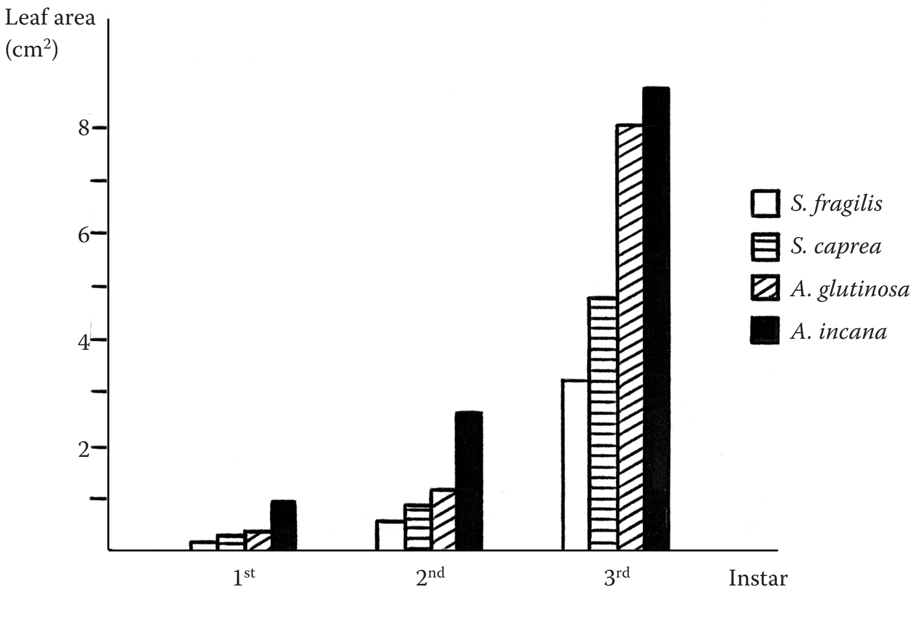

Fig. 8. Mean area of leaves of *S. fragilis*, *S. caprea*, *A. glutinosa* and *A. incana* damaged by larvae of the 1st to the 3rd instar of *G. lineola*. Laboratory examination, 1996 to 1998 and 2006

Table 5. Abundance of *G. lineola* imagoes in sweepings carried out on *A. glutinosa* and *A. incana* (Polnička, 1995). Mean leaf area of *A. glutinosa* damaged by imagoes and mean number of laid eggs in the laboratory. An asterisk* indicates the occurrence of *Beauveria bassiana*. In rearings free of infection, the total mean period of life is given of male and female imagoes in captivity. Field and laboratory examination, 1995

Date of trapping	Number of imagoes	Number of ♂♂/♀♀	Mean damaged area (cm²)	Mean number of laid eggs	Generation of imagoes	Mean life of ♂♂/♀♀ (days)
17 August	4	2/2	16.1	0	this year's	85/84
24 August	66	31/35	13.4	0	this year's	87/90
31 August	70	38/32	13.0	0	this year's	114/113
7 September	80	34/46	12.3	2.9	this year's	153/152
14 September	195	100/95	10.7	0	this year's	130/129
23 September	208	104/104	9.5	0	this year's*	35/34
4 October	111	58/53	8.1	7.6	this year's*	62/68
19 October	23	10/13	4.3	0	this year's*	27/26
3 December	2	1/1	3.8	0	this year's*	?
Total	759	378/381	–	–	–	(124/125)

Table 6. Weekly mortality of this year's imagoes of *G. lineola*. Weekly and total mean damaged leaf area of *A. glutinosa*. The beginning of egg laying. Imagoes were caught in Polnička on 24 August and 7 September 1995. Laboratory examination, 1995

Week	Period (from–to)	24 August (31 ♂♂ + 35 ♀♀)			7 September (34 ♂♂ + 46 ♀♀)		
		(number of ♂♂+♀♀/%)	(cm²/%)	(eggs/%)	(number of ♂♂+♀♀/%)	(cm²/%)	(eggs/%)
1st	24–30 August	66/0.0	335/37.9	–	?	?	?
2nd	31–6 September	65/1.5	120/13.6	–	?	?	?
3rd	7–13 September	63/4.5	41/4.6	–	80/0.0	273/27.7	–
4th	14–20 September	63/4.5	30/3.4	–	79/1.2	204/20.7	–
5th	21–27 September	62/6.1	33/3.7	–	76/5.0	103/10.4	–
6th	28–4 October	60/9.1	39/4.4	–	73/8.8	60/6.1	–
7th	5–11 October	54/18.2	50/5.7	–	69/13.7	38/3.9	–
8th	12–18 October	54/18.2	50/5.7	–	64/20.0	44/4.5	–
9th	19–25 October	53/19.7	63/7.1	–	63/21.2	40/4.0	–
10th	26–1 November	52/21.2	33/3.7	–	62/22.5	52/5.3	–
11th	2–8 November	50/24.2	60/6.8	–	61/23.8	34/3.4	–
12th	9–15 November	50/24.2	30/3.4	–	57/28.8	63/6.4	–
13th	16–22 November	*Beauveria bassiana*		92/100.0	55/31.2	75/7.6	134/100.0
Total		–	884/100.0	92/100.0	–	986/100.0	134/100.0
Mean		–	13.4	2.6	–	12.3	2.9

A. podanus (Sc.), *Olethreutes umbrosanus* (Frr.), *Cnephasia incertana* (Tr.), *C. stephensiana* (Doub.), *Eulia ministrana* (L.) (Tortricidae) and *Agonopteryx hypericella* (Hübn.) (Depressariidae) during a day (Urban 1983). Under heavy rain and wind, they also hide in fissures of bark, under fallen leaves etc.

This year's imagoes of the alder biological form caught on 17 August 1995 damaged on average 16.1 cm² leaves of *A. glutinosa* in the laboratory whereas imagoes caught on 3 November 1995 damaged only 3.8 cm² (Table 5). In the course of the first two weeks, feeding of imagoes was most intensive (about 50% of the total damaged area). Imagoes ingested food to a small extent until mid-November when the infection by *Beauveria bassiana* (Bals.) Vuill. occurred in rearings. In other rearings, 69% imagoes lived till 22 November when the rearing was finished (Table 6). Maturation feeding of this year's imagoes of the alder biological form takes in nature on average 3 weeks. Imagoes do not copulate and do not lay eggs before leaving for winter habitats. Under laboratory conditions, females laid eggs only sporadically, namely as late as in the second half of November (Table 6).

On the other hand, this year's imagoes of the alder biological form reared in the laboratory about 24 June 1996 (from eggs laid 16 May 1996) inten-

Table 7. Weekly area of leaves of *A. glutinosa* damaged by this year's imagoes of the alder biological form of *G. lineola* and the weekly number of laid eggs. Imagoes were reared in the laboratory on 24/6/1996 from eggs laid on 16/5/1996. Laboratory examination, 1996

Week	Period (from–to)	Damaged area		Laid eggs	
		(cm^2)	(%)	(number)	(%)
1st	24–30 June	30	18.1	0	0
2nd	1–7 July	55	33.2	83	21.3
3rd	8–14 July	36	21.7	156	40.0
4th	15–21 July	15	9.0	110	28.2
5th	22–28 July	10	6.0	41	10.5
6th	29–4 August	7	4.2	0	0
7th	5–11 August	5	3.0	0	0
8th	12–18 August	2	1.2	0	0
9th	19–25 August	2	1.2	0	0
10th	26–1 September	0	0	0	0
11th	2–8 September	1	0.6	0	0
12th	9–15 September	1	0.6	0	0
13th	16–22 September	1	0.6	0	0
14th	23–29 September	0	0	0	0
15th	30–6 October	0	0	0	0
16th <	7–27 October	1	0.6	0	0
Total		166	100.0	390	100.0
Number of ♂♂/♀♀		2/4			
Mean		27.7		97.5	
Mean life of ♂♂/♀♀ (days)		105/68			

sively damaged leaves of *A. glutinosa* for a period of 3 to 5 weeks. Until the end of October, they damaged on average 27.7 cm^2 leaves. About after a week feeding, they mated first and laid the first eggs. Within the 2nd and the 5th week, females laid on average 97.5 eggs. During August to November, imagoes died (Table 7). Interesting findings were obtained through rearing 5 males and 1 female, which hatched in the laboratory on 3 July 1998. These imagoes were reared from eggs laid on 27 May 1998 by last year's females. While females lived only 54 days, males lived on average 225 days (till February of the following year). Imagoes damaged on average 30.4 cm^2 leaves of *A. glutinosa* and females laid 687 eggs. In the period of the most intensive reproduction, they laid 240 eggs per week, i.e. 34.3 eggs per day (Table 8).

Through numerous laboratory studies it has been demonstrated that food consumption (assessed according to the damaged area of leaves) is much lower in males than in females. For example, this year's males of the willow biological form (reared from eggs on 21 June 2006) damaged on average 17.6 cm^2 leaves of *S. caprea*. They lived on average 140 days and produced on average 2,796 frass pellets of a total volume of 33.0 mm^3. Individually reared (unfertilized) females lived on average 162 days and damaged on average 30.9 cm^2 leaves (i.e. 1.8 times more than males). Females produced on average 5,085 frass pellets (i.e. 1.8 times more than males) of a total volume of 70.2 mm^3 (i.e. 2.1 times more than males) and laid on average only 182 eggs. However, imagoes reared in parent pairs (1 ♂:1 ♀) damaged on average 36.6 cm^2 *Salix caprea* (from 1 January 2007 other species of *Salix*) (i.e. 1.2 more than individually reared females). Males lived on average 122 days, females 131 days and produced together on average 5,353 frass pellets. Fertilized females laid on average 528 eggs (i.e. 2.9 times more than unfertilized females). It follows that imagoes of the same sex (without possibility of copulation) lived 1.1 to 1.2 times longer, but damaged on average 1.5 times smaller leaf area than imagoes living in co-educated rearings. Separately reared females laid nearly 3 times less eggs than imagoes in parent rearings (Table 9). Thus, the presence of individuals of the opposite sex markedly stimulates both feeding and reproduction of this year's imagoes. Nevertheless, some this year's fertilized as well as unfertilized females laid eggs at the end of year or at the beginning of the next year. It means that this year's females

Table 8. Results of the laboratory rearing of 6 this year's imagoes (5 males and 1 female) of the alder biological form of *G. lineola* on leaves of *A. glutinosa*. Imagoes were reared in the laboratory from eggs laid on 27 May 1998

Week	Period (from–to)	Damaged leaf area (cm^2)		Number of laid eggs	
		weekly	day-long	weekly	day-long
1st	3–9 July	40.3	0.96	0	0.0
2nd	10–16 July	27.5	0.65	112	16.0
3rd	17–23 July	16.5	0.39	175	25.0
4th	24–30 July	25.0	0.60	240	34.3
5th	31–6 August	24.0	0.57	114	16.3
6th	7–13 August	6.5	0.15	36	5.1
7th	14–20 August	7.0	0.17	10	1.4
8th	21–27 August	4.0	0.10	0	0.0
9th	28–3 September	2.0	0.06	–	–
10th	4–10 September	3.0	0.09	–	–
11th	11–17 September	2.5	0.07	–	–
12th	18–24 September	0.0	0.00	–	–
13th	25–1 October	2.0	0.06	–	–
14th	2–8 October	4.0	0.10	–	–
15th	9–15 October	4.0	0.10	–	–
16th	16–22 October	2.0	0.06	–	–
17th	23–29 October	2.0	0.06	–	–
18th	30–5 November	2.0	0.06	–	–
19th	6–12 November	5.0	0.14	–	–
20th	13–19 November	1.0	0.03	–	–
21st	20–25 November	2.0	0.06	–	–
Total		182.3	–	687	–
Mean		30.4	0.23	687	19.6

of the willow biological form of *G. lineola* do not tend to establish the 2nd generation even in the laboratory. It is also demonstrated by results of other numerous rearings of this year's imagoes (Tables 10 and 11). The tables also show that the average damaged leaf area on *S. caprea* is 1.4 to 1.7 times larger than on *S. fragilis*.

Generation conditions

Many-year studies have demonstrated that *G. lineola* has one-year development in Moravia. Only in the warmest parts of Moravia, a small population of this year's beetles can sexually mature still in the same year and establish the 2nd generation (Urban 1981). This year's imagoes of the alder biological form finish their feeding in the area of Žďár usually in October whereas imagoes of the willow form in the area of Brno already at the end of July and in August. According to Maisner (1974) this year's beetles search for hibernation shelters in August and September, according to Gharadjedaghi (1997) in September and at the beginning of October. However, literature data speak about 3 generations (Eckstein 1897) or even four generations per year (Nüsslin, Rhumbler 1922; Escherich 1923; Živojinovič 1948; Gäbler 1955; Koehler, Schnaider 1972 etc.). It is necessary to consider these statements to be improbable.

Under laboratory conditions, the alder biological form of *G. lineola* produced 2 generations on *A. glutinosa* and the willow biological form 3 generations on *S. fragilis* (Fig. 9) or even 4 generations per year (Tables 12 and 13). Already the 3rd generation of females laid eggs only minimally and the 4th generation not at all. Imagoes which did not lay eggs damaged on average 8 cm^2 leaves of *S. fragilis* before leaving for hibernation shelters. Fig. 10 depicts the average leaf area damaged by imagoes of the particular generations of the willow biological form on *S. fragilis* in 1999 (including the average number of laid eggs and the average life span). Fig. 11 demonstrates the same indicators (except the average life of imagoes). The figures show that the average leaf area of *S. fragilis* damaged by imagoes of the 1st generation was 21.0 cm^2 in 1999 and 22.8 cm^2 in 2006, i.e. the same or higher than in the last year's imagoes. Imagoes of

Table 9. Mean 14-day area of leaves of *S. caprea* (from 1 January to 5 January *S. alba* f. *vitellina pendula* Rehd., from 5 January to 23 January 2007 *S.* × *erythroflexuosa* Rag.) damaged by imagoes of the 1st generation of *G. lineola*. Mean 14-day number of frass pellets and laid eggs. Mean dimensions and volume of frass pellets. Imagoes were reared in the laboratory on 21 July 2006, namely from the stage of eggs. Hereafter, they were reared individually or in pairs. Laboratory examination, 2006 (2007)

Week	Period (from–to)	Males (6 indiv.)		Females (6 indiv.)			Males + females (4 + 4 indiv.)		
		mean damaged area (cm^2)	mean number of frass pellets	mean damaged area (cm^2)	mean number of frass pellets	mean number of eggs	mean damaged area (cm^2)	mean number of frass pellets	mean number of eggs
1st–2nd	21–4 July	8.8	1,446	10.7	1,560	46	9.7	1,600	52
3rd–4th	5–18 July	2.3	320	4.5	850	53	5.6	750	148
5th–6th	19–1 August	1.3	144	3.7	798	21	7.1	989	120
7th–8th	2–15 August	0.0	0.0	0.1	11	3	3.8	569	78
9th–10th	16–29 August	1.1	101	0.0	0	0	1.7	219	7
11th–12th	30–12 September	2.7	487	1.2	145	0	0.0	2	0
13th–14th	13–26 September	0.0	0.0	1.0	153	0	0.0	79	0
15th–16th	27–10 October	0.0	0.0	0.4	73	0	0.5	58	0
17th–18th	11–24 October	0.0	0.0	1.1	197	0	0.3	38	0
19th–20th	25–7 November	1.4	298	1.0	151	0	0.7	102	4
21st–22nd	8–21 November	0.0	0.0	0.0	0	0	2.4	249	44
23rd–24th	22–5 December	–	–	2.4	390	21	2.2	338	40
25th–26th	6–19 December	–	–	3.8	563	32	0.4	66	5
27th–28th	20–2 January	–	–	0.5	93	6	1.2	175	12
29th–30th	3–16 January	–	–	0.5	101	0	0.9	104	15
31st	17–23 January	–	–	–	–	–	0.1	15	3
Total		17.6	2,796	30.9	5,085	182	36.6	5,353	528
From–to		15.1–20.1	2,390–3,203	21.8–35.6	3,695–5,780	0–371	24.7–41.7	3,748–6,445	122–887
Mean length/width of frass pellets (mm)		0.687/0.148			0.750/0.153			–	
Mean volume of a frass pellet (mm^3)		0.0118			0.0138			–	
Volume of frass pellets (mm^3)		33.0			70.2			–	
Volume of frass pellets from 1 cm^2 (mm^3)		1.9			2.3			–	
Mean life (days)		140			162			122/131	

Table 10. Mean 14-day area of leaves of *S. caprea* and *S. fragilis* (from 1 January to 5 January 2007 *S. alba* f. *vitellina pendula* Rehd., from 5 January to 20 January 2007 *S.* × *erythroflexuosa* Rag.) damaged by imagoes of the 2nd generation of *G. lineola*. Mean 14-day number of frass pellets and laid eggs. Imagoes were reared in the laboratory. Laboratory examination, 2006 (2007)

Week	Period (from–to)	Hatching of imagoes 23. 7. 2006 *S. caprea* (3 ♂♂/3 ♀♀)			Period (from–to)	Hatching of imagoes 8. 9. 2006 *S. fragilis* (3 ♂♂/3 ♀♀)		
		mean damaged area (cm^2)	mean number of frass pellets	mean number of eggs		mean damaged area (cm^2)	mean number of frass pellets	mean number of eggs
1st–2nd	23–5 August	14.5	1,665	198	8–21 September	5.4	1,118	0
3rd–4th	6–19 August	7.1	1,144	155	22–5 October	0.5	68	0
5th–6th	20–2 September	0.5	80	0	6–19 October	1.8	318	0
7th–8th	3–16 September	0.0	0	0	20–2 November	0.5	78	0
9th–10th	17–30 September	0.0	0	0	3–16 November	0.4	80	0
11th–12th	1–14 October	1.4	214	0	17–30 November	2.4	410	42
13th–14th	15–28 October	0.0	5	0	1–14 December	3.2	517	58
15th–16th	29–11 November	0.6	78	0	15–28 December	0.8	127	2
17th–18th	12–25 November	0.0	0	0	29–11 January	0.3	50	0
19th–20th	26–9 December	0.4	98	0	12–18 January	0.0	0	0
21st–22nd	10–23 December	1.0	162	13	–	–	–	–
23rd–24th	24–6 January	0.5	91	8	–	–	–	–
25th–26th	7–20 January	0.2	72	0	–	–	–	–
Total		26.2	3,609	374	Total	15.3	2,766	102
Mean life (days)			80/103		Mean life (days)		77/100	

the 2nd generation damaged on average 20.0 cm^2 in 1999 and 19.0 cm^2 in 2006. A rapid decrease of food consumption was noted in imagoes of the 3rd and 4th generations. The average number of laid eggs was highest in imagoes after hibernation (360 in 1999 and 525 in 2006). In the next generations, the average number of eggs gradually decreased up to zero (in imagoes of the 4th generation). Based on the representative parallel study of the course of feeding and egg laying (carried out from October 2006 to January 2007) imagoes of the 3rd generation damaged on average 16.6 cm^2 leaves of *S. caprea* (and 15.4 cm^2 leaves of *S. fragilis*) and laid on average only 70.9 eggs on *S. caprea* (36.0 eggs on *S. fragilis*) (Table 14).

Natural enemies

Part 1 briefly discusses natural enemies of the last year's imagoes of *G. lineola* (Urban 2007). The development of larvae is particularly unfavourably

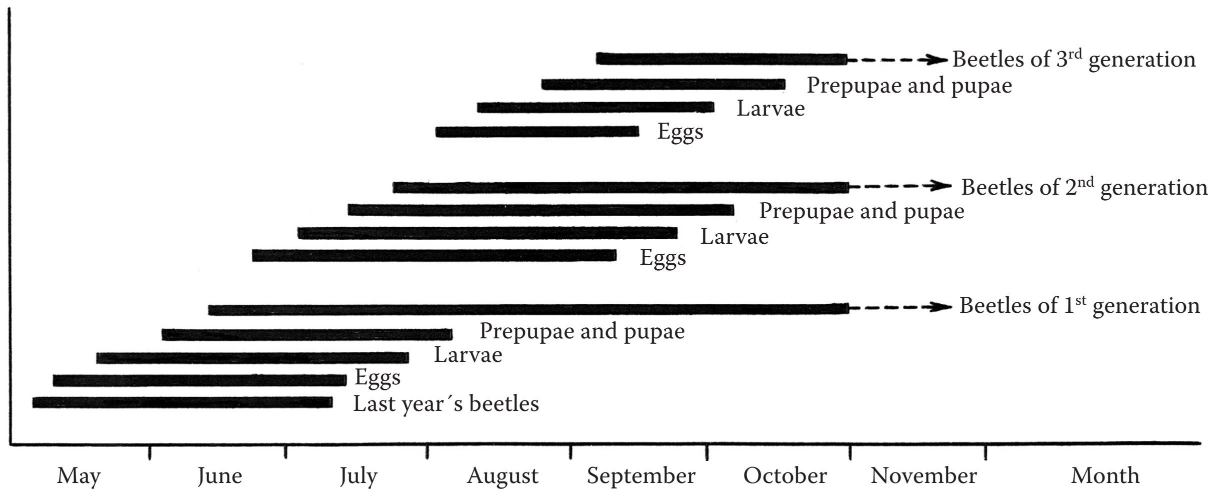

Fig. 9. The diagram of development of the willow biological form of *G. lineola* on leaves of *S. fragilis*. Laboratory rearing, 2006

Table 11. Mean 14-day area of leaves of *S. caprea* and *S. fragilis* (from 18 November to 29 December only *S. caprea*, later *S. alba* f. *vitellina pendula* Rehd. or *S.* × *erythroflexuosa* Rag.) damaged by this year's imagoes of *G. lineola*. Mean 14-day number of laid eggs. Imagoes were caught in Bílovice nad Svitavou on 29 July 2006. Laboratory examination, 2006 (2007)

Week	Period (from–to)	*S. caprea* (3 ♂♂/2 ♀♀)		*S. fragilis* (2 ♂♂/2 ♀♀)	
		mean damaged area (cm²)	mean number of eggs	mean damaged area (cm²)	mean number of eggs
1st–2nd	29–11 August	12.1	0.0	13.6	0.0
3rd–4th	12–25 August	1.3	0.0	0.0	0.0
5th–6th	26–8 September	1.7	0.0	0.3	0.0
7th–8th	9–22 September	0.7	0.0	0.0	0.0
9th–10th	23–6 October	0.6	0.0	2.2	0.0
11th–12th	7–20 October	0.8	0.0	1.0	0.0
13th–14th	21–3 November	1.2	0.0	0.0	0.0
15th–16th	4–17 November	0.9	7.0	0.0	0.0
17th–18th	18–1 December	3.9	82.5	0.0	0.0
19th–20th	2–15 December	2.2	83.0	0.2	0.0
21st–22nd	16–29 December	0.6	0.0	1.2	24.0
23rd–24th	30–12 January	0.0	0.0	0.5	2.0
25th	13–19 January	–	–	0.1	0.0
Total		26.0	172.5	19.1	26.0
Mean life (days)		130/145		97/146	

affected by dry weather worsening not only the embryogenesis and eclosion of egg larvae but also further development of larvae. Excessive dry weather impedes ecdysis, prolongs their development and increases mortality even by 30% (Brovdij 1973). Immature bodies of the 1st instar are most liable to drying up. Therefore, particularly young larvae often hedge against climate variations by means of hiding in various shelters. On suboptimal host species (e.g. on *S.* × *dasyclados*), larvae develop for a longer time and, therefore, they are subject to various predators more than on the trophically optimum *S. viminalis* (Häggström, Larsson 1995; Häggström 1997).

The larvae of *G. lineola* do not have (unlike some other species of chrysomelids) any dorsal defensive glands, but in the case of danger, they are able to move flatly by their tail. This defensive behaviour often malfunctions as evidenced by the very high mortality of larvae caused by common predators (e.g. various species of Heteroptera, Neuroptera, Aranea,

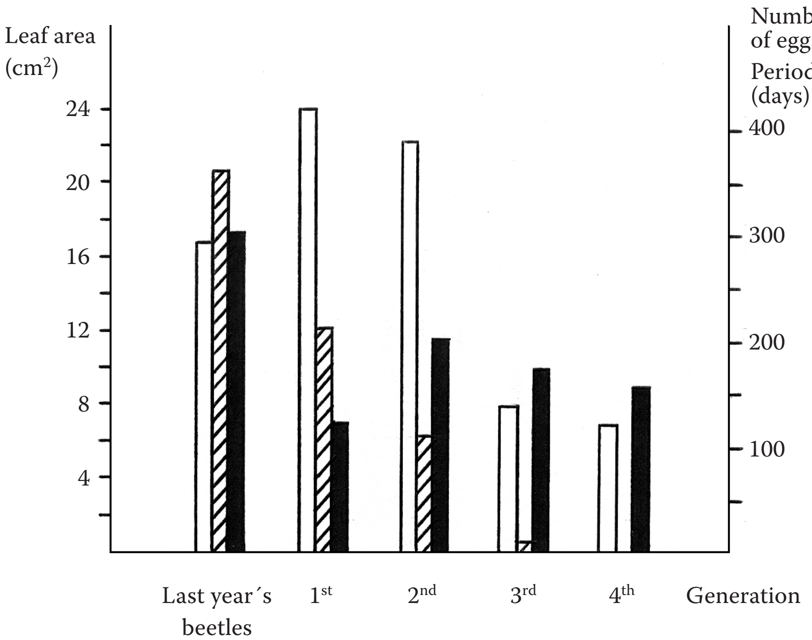

Fig. 10. Mean area of leaves of *S. fragilis* damaged by imagoes of the particular generations of *G. lineola* (light columns). Mean number of laid eggs (dash columns) and mean life of imagoes (dark columns). Laboratory examination, 1999

Table 12. Weekly area of leaves of *S. fragilis* (cm^2) damaged by *G. lineola* (numerator) and the weekly number of laid eggs (denominator). Imagoes were reared in the laboratory already from the egg stage. In rearings marked by an asterisk*, imagoes were caught at the beginning of maturation feeding in nature. Question marks indicate the period of hibernation of imagoes under external conditions. The period of hibernation and the period of rearings in April to May 2000 are included into the mean period of life (days). Laboratory examination, May to December, 1999

Week	Imagoes reared in the laboratory (*imagoes caught in nature)/generation							
	10 May*/ last year's	19 June/1st	21 June/1st	24 June/1st	27 June/1st	27 June/1st	4 August/ 2nd	4 August/ 2nd
1st	7/98	43/0	29.5/0	69/54	26.3/0	62/28	29/0	12.2/51
2nd	10/117	14.5/0	6/0	60/312	5.3/0	36/252	6/24	5.3/56
3rd	7.6/110	10/91	2.3/0	53/440	5.4/0	26/179	5.6/64	3.5/33
4th	3.8/34	17/75	0	43/345	12.5/28	22/204	3.2/26	3.1/22
5th	1.2/–	23.5/235	1.5/0	23/41	12.5/108	12.5/45	1.7/0	4.5/0
6th	1.6/–	21/170	2.6/0	7/13	10/38	9.4/0	0	0
7th	0.7/–	8/60	2.2/0	9/0	7.1/0	8/0	2/0	0.5/0
8th	1.5/–	8.5/49	0.6/0	7.4/0	6/–	12/0	1.3/0	1/0
9th	0/–	4/10	2.8/0	5/0	4.2/–	3.4/0	0	1.4/0
10th	–	25/0	0	1/0	3/–	6.5/0	3/0	0
11th	–	2/0	0	0	0.1/–	2.7/0	0	0.1/0
12th	–	0	0.7/0	0	4/–	1/0	0	0
13th	–	3.5/0	8/0	2/0	2/–	1.3/0	0	0
14th	–	2/0	1/0	0.5/0	1.3/–	3.6/0	?	?
15th	–	0	2.2/0	0	2.5/–	0	?	?
16th	–	0	2/0	1/0	0/–	0.5/0	?	?
17th	–	1.1/0	1.5/0	1.5/0	0/–	1/0	?	?
18th	–	3/0	2.5/0	0	0/–	1/0	?	?
19th	–	0.3/0	0	0	0/–	4.5/0	?	?
20th	–	?	0	?	?	2/30	?	?
21st	–	?	0	?	?	9/56	?	?
22nd	–	?	0	?	?	4.5/58	?	?
Total	33/359	164/690	65/0	282/1,205	102/174	229/852	52/114	32/162
Number of ♂♂/♀♀	1/1	4/3	4/1	8/6	4/1	6/3	–/4	1/1
Mean	17/359	23/230	13/0	20/201	20/174	25/284	13/29	16/162
Mean life of ♂♂/♀♀ (days)	56/30	182/146	308/315	41/111	111/44	88/98	–/238	180/160

Formicoidea etc.). For example, parasitic chalcid flies of the genus *Tetrastichus* Hal. (Eulophidae) destroy up to 50% eggs in Ukraine (Brovdij 1973).

Under laboratory conditions this year's imagoes of the alder biological form of *G. lineola* caught in Polnička during August–November 1995 were often attacked by the fungus *Beauveria bassiana* (Bals.) Vill. after 1 to 3 months. This year's imagoes of the willow biological form caught in Bílovice nad Svitavou in 1999 were seldom infected by the fungus *Fusarium ventricosum* Appel & Woll. Also larvae of the 3rd instar were sporadically infected by the fungus *B. bassiana* in 1999 (det. by Dr. L. Marvanová, Brno).

This year's imagoes of the willow biological form of *G. lineola* were 45 to 65% parasitized by *Medina collaris* (Fall.) (Tachinidae) (det. by Prof. J. Vaňhara, Brno) in Bílovice nad Svitavou in July and August 2006. Imagoes of *M. collaris* hatched partly in August of the same year (after on average 10-day duration of puparia), partly in the next year after overwintering. In 1975 in an osier plantation in Prosenice (former Přerov district), a small part (about 2%) of this year's imagoes was infected by helminths of the family Mermithidae (Nematoda) (det. by Prof. I. Rubcov, Saint Petersburg) (Urban 1981). Parasitized individuals occurred on shoots of willows in the

Table 13. Weekly area of leaves of *S. fragilis* (cm^2) damaged by imagoes of *G. lineola* (numerator) and the weekly number of laid eggs (denominator). Imagoes reared in the laboratory already from the egg stage. Question marks indicate the period of hibernation of imagoes under external conditions. The period of hibernation and the period of rearings in April to May 2000 are included into the mean period of life (days). Laboratory examination, August to December, 1999

Week	Imagoes reared in the laboratory/generation							
	8 August/2nd	10 August/2nd	11 August/2nd	12 August/2nd	21 September/3rd	26 September/3rd	27 September/3rd	16 November/4th
1st	4.9/23	54.5/59	76/20	19.1/55	31/0	10.5/–	25/0	4.5/0
2nd	4.3/45	20/195	38/251	10/93	11/10	7/–	24/30	7/0
3rd	4.1/51	15.5/169	29/219	6.7/114	0	–	10/15	3/0
4th	3.5/36	11.4/35	12/72	12/150	0	–	1/0	?
5th	1/0	0	9/0	13.2/113	0	–	0.3/0	?
6th	0	0	4/0	10.5/38	?	?	?	?
7th	0	1.5/0	2/0	2/36	?	?	?	?
8th	0	7/0	1/0	0.1/0	?	?	?	?
9th	0	0.8/0	2.5/0	0.1/0	?	?	?	?
10th	0	2.2/0	0.6/0	0	?	?	?	?
11th	0	4/0	10/0	4/0	?	?	?	?
12th	0	6/0	6/0	0.5/0	?	?	?	?
13th	?	6/0	4/0	0	?	?	?	?
14th	?	3/0	29/21	0	?	?	?	?
15th	?	4/0	29/134	?	?	?	?	?
16th	?	4.3/25	16/86	?	?	?	?	?
17th	?	0.2/0	5/0	?	?	?	?	?
18th	?	?	?	?	?	?	?	?
Total	18/155	140/483	273/803	78/599	42/10	17/0	60/45	14/0
Number of ♂♂/♀♀	–/1	3/4	6/7	–/3	2/3	2/0	6/2	1/1
Mean	18/155	20/121	21/115	26/200	8/3	9/–	7/23	7/0
Mean life of ♂♂/♀♀ (days)	–/144	280/250	188/165	–/117	192/213	208/–	119/237	179/135

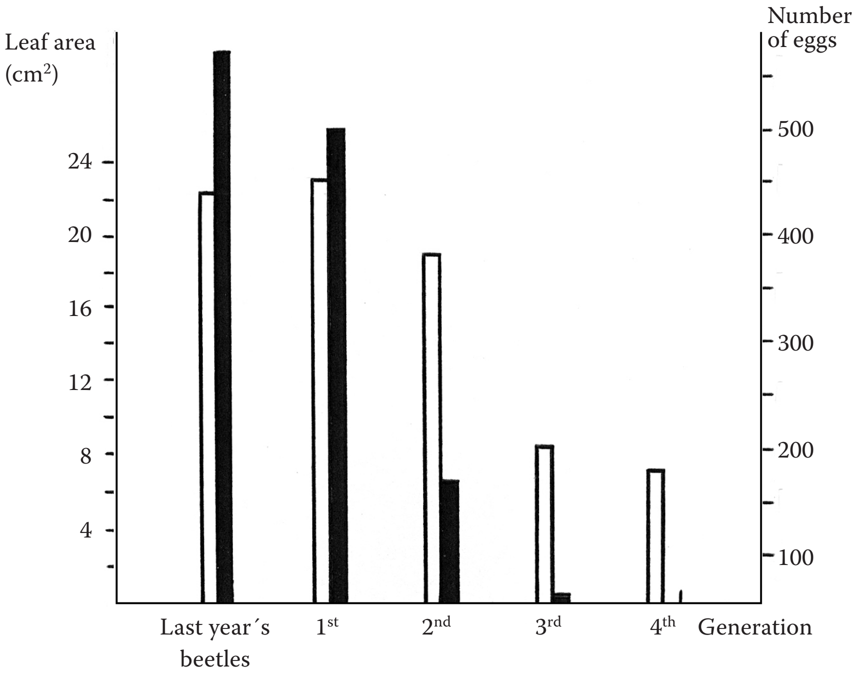

Fig. 11. Mean area of leaves of *S. fragilis* (*S. caprea*) damaged by imagoes of the particular generations of *G. lineola* (light columns). Mean number of laid eggs (dark columns). Laboratory examination, 2006

2nd half of September and at the beginning of October, i.e. at the time when all healthy beetles were already hidden in winter shelters. In addition to insect predators, beetles of *G. lineola* are killed e.g. by Aves, Amphibia, Reptilia, Insectivora, Chiroptera etc.

Harmfulness

Galerucella lineola is an important pest of osier plantations (Escherich 1923; Tuinzing 1946; Kovačevič 1957; Wagner, Ortmann 1959; Urban 1981; Kendall et al. 1996; Höglund et al. 1999; Sage et al. 1999 etc.). In Armenia it is considered to be a pest of forest nurseries (Arnoldi et al. 1955), in Ukraine a pest of willows and alders (Brovdij 1973) and in Iran a pest of alders (Sadeghi et al. 2004). In Norway the chrysomelid damages *A. glutinosa*, which was abundantly used there as a food for cattle in the past.

The last year's (parent) beetles colonize ends of intensively growing shoots in spring. During 2.5 to 3-month maturation and regeneration feeding, they damage on average 22.6 cm^2 *A. glutinosa* or *S. caprea.* From the 3rd decade of May or from the beginning of June, larvae also begin to take part in the defoliation of newly unfolded leaves. During a 3 to 4-week devel-

Table 14. Mean 14-day area of leaves of *S. caprea* and *S. fragilis* (from 11 November to 31 December 2006 only *S. caprea*, later *S. alba* f. *vitellina pendula* Rehd. or *S.* × *erythroflexuosa* Rag.) damaged by imagoes of the 3rd generation of *G. lineola*. Mean 14-day number of laid eggs. Imagoes were reared in the laboratory. Laboratory examination, 2006 (2007)

Week	Period (from–to)	Hatching of imagoes 16. 9. 2006 *S. caprea* (14 ♂♂/15 ♀♀)		Hatching of imagoes 16. 9. 2006 *S. fragilis* (9 ♂♂/10 ♀♀)	
		mean damaged area (cm^2)	mean number of eggs	mean damaged area (cm^2)	mean number of eggs
1st–2nd	16–29 September	6.7	0.0	6.9	0.0
3rd–4th	30–13 October	0.1	0.0	0.0	0.0
5th–6th	14–27 October	0.8	0.0	1.1	0.0
7th–8th	28–10 November	1.2	0.0	1.2	0.0
9th–10th	11–24 November	0.8	0.0	1.1	0.0
11th–12th	25–8 December	2.6	26.5	1.9	15.9
13th–14th	9–22 December	2.8	25.5	2.3	17.3
15th–16th	23–5 January	1.3	14.7	0.6	2.8
17th–18th	6–19 January	0.3	4.2	0.3	0.0
Total		16.6	70.9	15.4	36.0
Mortality of ♂♂/♀♀ (19 January 2007) (%)		33.3/30.0		57.1/33.3	

opment, the larvae damage on average 9.7 cm^2 leaves of *A. glutinosa* (i.e. 2.3 times less than the last year's beetles) or 6.0 cm^2 leaves of *S. caprea* (i.e. 3.8 times less than the last year's beetles). From the end of June to the end of August (in the alder biological form in the Žďár area from mid-July to the end of October), this year's beetles occur on young leaves. They damage on average 16.1 cm^2 leaves of *A. glutinosa* or 12.0 cm^2 leaves of *S. caprea*. During outbreak, starving beetles feed also on buds and fine bark of shoots. A reduction of increments and sometimes also shoot decline occur as a result of decreasing the assimilatory area and even defoliation or bark and bud browsing.

Possibilities of protection and control

Beetles of *G. lineola* can be effectively controlled by insecticides, namely in spring after the invasion onto host trees has ended. A control measure has to be carried out at the latest within a week after the beginning of maturation feeding, i.e. when females did not yet begin to lay eggs. Sexually mature females can be easily identified according to the enlarged abdomen, which slightly overhangs the ends of wing-cases. If an opportune date of the measure is chosen, it is usually possible to kill also imagoes of other numerous herbivorous species (e.g. harmful species of Chrysomelidae, Curculionidae, Attelabidae, Tenthredinidae etc.). In the study of post-hibernation dispersion of *G. lineola* in bioenergy plantations in Great Britain beetles were found to colonize the margins of plantations first (Sage et al. 1999). Along the margins of the plantations, 80% beetles occurred within an 8 m zone. According to the authors, this fact can be used for the integrated control of the pest with relatively small doses of insecticides.

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ABSTRAKT: Druhá část práce pojednává o vývoji a škodlivosti larev a o úživném žíru letošních brouků *Galerucella lineola* (F.) před odchodem do zimovišť. Embryogeneze trvá průměrně 12 (v laboratoři devět) dnů. Ve výše položené studenější vyšetřované oblasti na Žďársku se larvy olšové biologické formy vyskytují na *Alnus glutinosa* a *A. incana* v červnu až srpnu. V teplejší nížinné oblasti na Brněnsku se larvy vrbové formy vyskytují na *Salix triandra*, *S. viminalis* a *S. caprea* od třetí dekády května do začátku srpna. V laboratoři se larvy olšové formy vyvíjely průměrně 16 dnů a larvy vrbové formy 13 dnů. Larvy olšové formy poškodí průměrně 9,7 cm^2 listů *A. glutinosa* a larvy vrbové formy 6 cm^2 listů *Salix caprea*. Letošní imaga se na Žďársku vyskytují na olších od poloviny července do konce října a během tří týdnů poškodí průměrně 16 cm^2 listů *A. glutinosa*. Letošní imaga se na Brněnsku vyskytují na vrbách od konce června do konce srpna a během dvou týdnů poškodí průměrně 12 cm^2 listů *S. caprea*. Vývoj je univoltinní (v jižních částech Moravy částečně bivoltinní). Olšová forma mandelinky vytvářela v laboratoři dvě (vrbová dokonce až čtyři) neúplné generace. Letošní imaga poškodila průměrně 36,6 cm^2 *S. caprea* a vykladla 122 až 887 (průměrně 528) vajíček. Imaga vrbové formy byla na Brněnsku až ze 65 % parazitována *Medina collaris* (Fall.) (Tachinidae).

Klíčová slova: Chrysomelidae; *Galerucella lineola*; vývoj larev; žír letošních brouků; generační poměry; přirození nepřátelé; škodlivost

Corresponding author:

Prof. RNDr. Ing. Jaroslav Urban, CSc., Mendelova zemědělská a lesnická univerzita v Brně, Lesnická a dřevařská fakulta, Lesnická 37, 613 00 Brno, Česká republika
tel.: + 420 545 134 121, fax: + 420 545 211 422, e-mail: urbanj@mendelu.cz