Some sawfly larvae survive predator-prey interactions with pentatomid *Picromerus bidens*

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Abstract

Most Asopinae stinkbugs (Hemiptera: Pentatomidae) prey on other insects, including sawfly larvae (Hymenoptera: Symphyta). Sawfly larvae of the Argidae and Pergidae contain toxic peptides, but whether they are defended against stinkbugs remains poorly studied. A literature survey indicates that no publication is devoted to laboratory tests specifically using these sawflies against stinkbugs. Here, laboratory bioassays were made with the stinkbug *Picromerus bidens* and four sawfly species at last larval instars: *Arge ochropus* (Argidae), *Arge pagana* (also tested at medium instars), *Lophyrotoma zonalis* (Pergidae), and *Allantus rufocinctus* (Tenthredinidae). Following 24 h of possible predator-prey interactions, no larvae of *A. rufocinctus* survived, whereas most or all larvae of the other sawfly species did survive and were still alive 48 h later. When feeding on an argid or pergid larva, the feeding periods lasted on average 6–20 s only, some bugs removing their rostrum and abruptly backing away. Full-grown larvae of *A. pagana* were attacked less than younger ones. It is likely that the tested Argidae and Pergidae are well defended against *P. bidens* by potent, internal antifeedants, while defensive body movements combined with a large body size play a secondary role.

Keywords Argidae; Pergidae; Bioassays; Antifeedant; Chemical defence

Introduction

Asopinae stinkbugs (Hemiptera: Pentatomidae) are important predators, especially of lepidopteran, coleopteran and hymenopteran (De Clercq 2000). Stinkbugs include generalist predators living in various habitats, but also more specialized species occurring in a few habitats where prey species diversity is rather low. Stinkbugs on a preferred host plant may specialize, at least temporarily, on phytophagous prey species related to these plants. Thus, most stinkbugs are opportunistic in their food preferences. This is the case for *Picromerus bidens* (Linnaeus, 1758) which feeds on several insect orders (De Clercq 2000).

Sawfly larvae are phytophagous hymenopterans preyed upon by many predators, and they are defended by a diversity of defence mechanisms often based on chemicals (Boevé et al. 2013). Most species among the sawfly families Argidae and Pergidae contain toxic peptides that are lethal to mammals and assumed to be distasteful to invertebrate predators such as ants (Petre et al. 2007; Boevé et al. 2014). No studies, however, have specifically considered the effectiveness of such chemical defences on attacking stinkbugs. Published field observations and laboratory tests on stinkbugs–sawfly larvae interactions are often related to sawflies of economic importance, typically as forest pests with an eye toward using stinkbugs for biocontrol (De Clercq 2000; Table 1).

Here, literature references were compiled into a list (Table 1), to introduce and complement a discussion about bug-sawfly interactions. Laboratory bioassays were performed in which two argid, one pergid and one tenthredinid species were offered to *P. bidens*. The predator-prey interactions and survival rates of both antagonists were recorded. The potential impact of the toxic peptides on the stinkbugs is discussed.

Materials and Methods

Laboratory bioassays were performed with sawfly larvae collected in the field and maintained in plastic boxes containing fresh leaves of their host plant. Four sawfly species were collected: the argids *Arge pagana* (Panzer, 1797) and *Arge ochropus* (Gmelin, 1790) in Uccle, Belgium, on *Rosa* sp. (Rosaceae), the pergid *Lophyrotoma zonalis* (Rohwer, 1910) in Brisbane, Australia, on *Melaleuca quinquenervia* (Cav.) S.T.Blake, 1958 (Myrtaceae), and the tenthredinid *Allantus rufocinctus* (Retzius, 1783) in Uccle on *Rosa* sp. The sawfly larvae were tested during their last larval instar, which corresponds to instar V or VI (L5-6) in *A. pagana* (see Petre et al. 2007). This species was also tested at instar III to V (L3-5). Thus, four test groups were used plus the tenthredinid as a control group.

Picromerus bidens individuals were received at the end of nymphal instar IV from a rearing maintained at Ghent University (Belgium). They received caterpillars of *Galleria mellonella* (Linnaeus, 1758) as food. Bugs having reached the adult stage (instar V) during the night were isolated in the morning and kept without food. These individuals were used in the test only once, five hours after isolation. The bugs were maintained in a climate chamber at 15–20 °C during day and night, but at 20–25 °C during the day of testing.

Sawfly larvae were tested in cylindric plastic containers of 3 cm diameter and 7 cm height, with a 1 cm thick moistened plaster layer on the bottom. The test started (t = 0) by placing a single sawfly larva in the plastic container, together with a piece of host-plant leaf, and by adding one bug to each container. This test was replicated 18 times for each sawfly species/instar. The reactions of both larva and bug were noted from t = 0 to 30 min (observation period), and the number and time of bug attacks were recorded. The length of each attack was measured from the introduction of the stylet in the larval body to its removal. After the observation period, the test continued up to t = 24 h (interaction period). The survival of both the larvae and bugs was recorded at t = 24, 48, and 72 h (i.e. day 1 to 3).

Two statistical tests were computed online: an Analysis of variance from summary data (Merser and Pezzullo 2020) to compare bug feeding times across the four test groups, and a Fisher exact probability test (Lowry 2020) to examine the influence of body size within *A. pagana* on bug attacks.

Results

Picromerus bidens showed no signs of intoxication during or after the observation period, and most if not all of them were still alive at t = 3 days (Table 2). Some bugs however removed their rostrum and abruptly backed away when feeding on the larval content of *A. pagana* L3-5, L5-6, or *A. ochropus*. Such a sudden rejection of a prey was never observed with the sawfly larva of *A. rufocinctus*. Once it was pierced, the stinkbug never removed its stylet from *A. rufocinctus*.

Allantus rufocinctus and *L. zonalis* larvae hardly moved when attacked by a bug. The larvae of *A. pagana* L3-5 and L5-6 generally did not react when first approached and/or attacked. But some larvae of this species were able to stop persistent attacks for a while by moving their abdomen towards the bug. Compared with *A. pagana*, *A. ochropus* made more violent movements of the abdomen when approached and/or attacked by a bug.

During the observation period, 10 out of 18 *A. rufocinctus* larvae were attacked by a bug that pierced the larva only once (Fig. 1). Nine of these feeding events extended beyond the half an hour of observation, making it impossible to calculate a mean feeding time for this sawfly species. Feeding events lasted from 1–300 s for the four test groups, with an average feeding time per group of 6–20 s (Table 2, Fig. 1). The values per group were not significantly different ($F = 2.091$, $P = 0.106$, $N = 4$; Analysis of variance from summary data). More larvae of *A. pagana* were attacked at L3-5 (14 out of 18) than L5-6 (4 out of 18) ($P = 0.002$, Fisher exact probability test), and they were attacked more often (Fig. 1).

Similarly, the bugs attacked more, and more often, larvae of *A. ochropus* than those of *L. zonalis*.

Following the end of the interaction period, no larva of *A. rufocinctus* survived (N = 18), whereas 89–100% of the other sawfly species/instars survived (N = 18 four times; Table 2).

Discussion

At the end of the interaction period with the bug *P. bidens*, nearly all larvae of *A. pagana*, *A. ochropus* and *L. zonalis* were alive, whereas all *A. rufocinctus* larvae were dead. Since ten out of 18 larvae of this species were attacked during the observation period, the other ones were most probably attacked afterwards. Similarly, it is likely that for *A. pagana* L5-6 and *L. zonalis* several larvae were first attacked after the observation period. In any event, the high survival rate in the four test groups contradicts the statement that "All [prey] larvae bitten or sucked even very slightly [by *P. bidens*] are doomed to certain death" (Mayné and Breny 1948, p. 203).

The bugs that attacked a larva of *A. ochropus* or *A. pagana* L3-5 fed at least twice on average, indicating that they were hungry. Their feeding time was similar across the four test groups and did not exceed 20 s on average. This is surprisingly short compared with the feeding time on *A. rufocinctus*, and feeding on other insects can last hours (Javahery 1986). Moreover, feeding trials here could end abruptly with the bug suddenly distancing itself from the larva.

Many sawfly larvae use chemicals in anti-predator defences, but they are preyed upon by bugs anyway. The Nematinae (Tenthredinidae) emit volatiles from ventral glands, whereas other tenthredinids especially among the Blennocampinae and Athaliinae easily bleed hemolymph containing harmful plant-derived compounds (Boevé et al. 2013). The Diprionidae as well as the Perginae and Pergulinae (Pergidae) regurgitate an entangling oily fluid (Eisner et al. 1974; Morrow et al. 1976; Pereira et al. 2008). A literature survey indicates, however, that hemipteran predators are frequently recorded preying on Diprioninae (Diprionidae) in field and/or laboratory conditions (Table 1). Some tenthredinids are less easily preyed upon, but the influence and value of specific protective chemicals against bug predation remain unclear. A few publications mention Pentatomidae and a Reduviidae feeding on Argidae or Pergidae larvae, but whether toxic peptides occur in these sawflies is not always known (Table 1). Furthermore, the asopine *Podisus maculiventris* (Say, 1832) clearly rejected larvae of *A. pagana* (own laboratory observations).

The aforementioned short feeding time and sudden rejection by the bugs suggest the existence of an internal chemical defence in the tested Argidae and Pergidae species. The total quantities of toxic peptides are ca. 50 μg per larva in *A. ochropus*, 75–80 μg per larva in *A. pagana* L5-6, and 1300–1500 μg per larva in *L. zonalis* (Boevé et al. 2014), whereas no data exist about chemical compounds that would be used in defence by *A. rufocinctus* and *A. pagana* L3-5. Toxic peptides are predominantly detected in the integument and hemolymph of *A. pagana* and *L. zonalis* (Boevé and Rozenberg 2020). Thus, the toxins from the hemolymph probably inhibited stinkbug feeding.

Larvae of *A. pagana* were more often attacked at L3-5 than L5-6, which may be explained by a larger body size and/or a greater effectiveness of body movements in the older larvae. *Arge pagana* L5-6 and *L. zonalis* were less often attacked than the other test groups, suggesting that a larger larval body size hampered the stinkbug attacks. Indeed, *P. bidens* prefers small to medium-sized and slow moving prey items (Mayné and Breny 1948; Javahery 1986). Generally, body movements are like a double-edged sword from a prey's perspective. They stimulate the predator to attack (Javahery 1986) while they can also physically repel and dislodge predators, especially small ones such as invertebrates. Conversely, some sawfly larvae remain immobile even if attacked (Boevé et al. 2013). Here, a large body size combined with body movements may have partially mitigated predation risks. Asopines generally dislike hairy prey (Whitmarsh 1916; Oetting and Yonke 1971; Senrayan and Ananthakrishnan 1991) and they encounter difficulties in attacking gregarious prey species (Tostowaryk 1972; Morrow et al. 1976; McClure and Despland 2011). Since nearly all larvae of the four test groups survived the bioassays, body size and movements appear to be of secondary importance in the defensive strategy of Argidae and Pergidae larvae containing toxic peptides.

Non-chemical factors probably play a greater role in natural conditions than in the present experimental conditions where sawfly larva and stinkbug were closely confined, during 24 h. The overall defensive effectiveness in nature is expected to increase accordingly. At an ultimate level, however, it is assumed that the evolution of gregariousness and body appearance has been driven by the presence of the toxins in these two sawfly families (Boevé et al. 2018a). Generally, the bioassay results presented here and published data about bug–sawfly interactions suggest that these toxins constitute a rare and potent antifeedant at least against *P. bidens*. This conclusion should be confirmed by further research that directly tests the toxins on stinkbugs.

Compliance with ethical standards – Declarations

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Table 1 Literature data about interactions between sawfly larvae and hemipteran predators

Sawfly family/ subfamily	Sawfly species (= synonym)	Hemiptera	Data and observations (original reference)	Condi-tion	Sawfly defence	Reference
Argidae						
Arginae	*Arge salicis* Rohwer, 1912 (= *Hylotoma pectoralis*)[1]	"pentatomid"	A single bug species observed to suck half-grown larvae	Field	–	(Schwarz 1909)
Diprionidae						
Diprioninae	*Microdiprion pallipes* (Fallén, 1808) (= *Diprion* (*Microdiprion*) *pallipes*)	*Picromerus bidens*	Bugs destroy 30-40% of larvae	Field	–	(Mallach 1974)
Diprioninae	*Diprion similis* (Hartig, 1836) (= *Diprion simile*)	*Picromerus bidens*	Two bug specimens preying on larvae	Field	–	(Lattin and Donahue 1969)
Diprioninae	*Diprion similis*	*Podisus serieventris*, *P. placidus*, *P. modestus, P. maculiventris*	Bugs commonly feed on larvae in the field, and were reared on larvae	Field & lab	–	(Coppel and Jones 1962)
Diprioninae	*Gilpinia frutetorum* (Fabricius, 1793)	*Picromerus bidens*	Bugs feed on larvae	Field	–	(Kelton 1972)
Diprioninae	*Neodiprion excitans* Rohwer, 1921	*Arilus cristatus* (Reduviidae), *Podisus fretus*	Predators of the larvae included a heavy population of the wheel and pentatomid bug	Field	–	(Hetrick 1959)
Diprioninae	*Neodiprion lecontei* (Fitch, 1858)	*Apateticus bracteatus*, *Apiomerus crassipes* (Reduviidae), *Arilus cristatus* (Reduviidae), *Nabis ferus* (Nabidae), *Podisus serieventris*, *Pselliopus cinctus* (Reduviidae), *Sinea diadema* (Reduviidae), *Zelus socius* (Reduviidae), *Apateticus* sp., *Podius* sp.	Association	Field	–	(Benjamin 1955)
Diprioninae	*Neodiprion nanulus* K. Schedl, 1933 (= *Neodiprion nanulus nanulus*)	*Euschistus variolarius*	A bug was collected feeding on a fifth instar larva	Field	–	(Kapler and Benjamin 1960)
Diprioninae	*Neodiprion pinetum* (Norton, 1869)	*Podisus placidus*	Bugs preying on sixth instar larvae	Field	–	(Rauf and Benjamin 1980)
Diprioninae	*Neodiprion pratti* (Dyar, 1899)	*Apiomerus crassipes* (Reduviidae), *Pselliopus cinctus* (Reduviidae), *Podisus maculiventris*	The bugs attacked mature larvae	Field	–	(Knerer and Wilkinson 1990)
Diprioninae	*Neodiprion rugifrons* Middleton, 1933	*Podisus maculiventris*	Predation on larvae by stinbugs, especially *P. maculiventris*, influences sawfly populations	Field	–	(Wilkinson et al. 1966)

Diprioninae	*Neodiprion sertifer* (Geoffroy, 1785) (= *Diprion sertifer*)	*Picromerus bidens*	Sawfly infestation probably stopped by the bugs that suck out larvae	Field	–	(Forsslund 1944)
Diprioninae	*Neodiprion sertifer*	*Podisus placidus*	Bug is a larval predator associated with the sawfly	Field	–	(Benjamin et al. 1955)
Diprioninae	*Neodiprion sertifer*	*Rhynocoris annulatus* (Reduviidae)	Bug repeatedly observed emptying larvae	Field	–	(Niklas and Franz 1957)
Diprioninae	*Neodiprion swainei* Middleton, 1931; *N. pratti banksianae* Rohwer, 1925	*Podisus modestus*	Bugs usually attacks on the periphery of sawfly colonies	Field?	–	(Tostowaryk 1971a)
Diprioninae	*Neodiprion swainei*	*Pilophorus uhleri* (Miridae)	Bug as a predator of larvae at instar I & II (Smirnoff 1959)	Field?	–	(Coppel and Benjamin 1965)
Pamphiliidae						
Pamphiliinae	*Pamphilius betulae* (Linné, 1758)	"bug"	Two bugs killed each one a larva	Field?	–	(Vikberg 2002)
Pergidae						
Perginae	*Pseudoperga guerinii* (Westwood, 1880) (= *Pseudoperga guerini*)[2]	*Leana australis* (Reduviidae)	Bug adult sometimes can attack a single larva of a sawfly colony	Field	+/–	(Morrow et al. 1976)
Pergulinae	*Haplostegus nigricrus* Conde, 1936	*Podisus nigrispinus*, *Supputius cincticeps*, *Brontocoris tabidus*	All *P. nigrispinus* and *S. cincticeps* died within 24 h after contact with regurgitated compounds from the larvae, whereas *B. tabidus* survived until adult stage	Lab	+/–	(Pereira et al. 2008)
Perreyiinae	*Heteroperreyia hubrichi* Malaise, 1955[3]; *Heteroperreyia kava* D.R. Smith, 2019 (= *Heteroperreyia* sp.)[1,4]	*Brontocoris tabidus*	Bug nymphs and adults feeding on larvae	Field	–	(Mc Kay et al. 2019)
Tenthredinidae						
Allantinae	*Monostegia abdominalis* (Fabricius, 1798)	*Podisus modestus*	Bugs attacked larvae, but only in no-choice tests, and rejected them after a few minutes only	Lab	+	(Tostowaryk 1971b)
Athaliinae	*Athalia rosae* (Linné, 1758)	*Podisus maculiventris*	≥5O% Larvae alive or killed but not emptied after exposure to bug	Lab	+/–	(Boevé and Müller 2005)
Athaliinae	*Athalia rosae*	*Podisus maculiventris*	Sequestration of plant glucosinolates by larvae only marginally affects the development of the bug	Lab	–	(Van Geem et al. 2014)
Blennocampinae	*Phymatocera aterrima* (Klug, 1816)	*Picromerus bidens*	Bug nymph feeds on larvae	Field	–	(Butler 1923)
Blennocampinae	*Phymatocera aterrima*, *Rhadinoceraea aldrichi* (MacGillivray, 1923), *R. micans* (Klug, 1816)[5], *R. nodicornis* Konow, 1886	*Podisus maculiventris*	≥5O% Larvae alive or killed but not emptied after exposure to bug	Lab	+/–	(Boevé and Müller 2005)
Heterarthrinae	*Caliroa cerasi* (Linné, 1758)	*Picromerus bidens*	Bug nymphs prefer young larvae; bug adults attack and kill all larval stages	Lab	–	(Carl 1976)

Heterarthrinae	*Caliroa cerasi*	*Brontocoris nigrolimbatus*	Bug nymphs I-V consume a mean of 33 sawfly larvae, a bug adult about 146 ones	Field & lab	–	(Rebolledo et al. 2004)
Nematinae	*Euura pavida* (Serville, 1823) (= *Nematus pavidus*)	*Podisus maculiventris*	≥5O% Larvae alive or killed but not emptied after exposure to bug	Lab	+/–	(Boevé and Müller 2005)
Nematinae	*Nematus* spp.	*Picromerus, Podisus*	Bugs feeding on larvae, e.g. 1 larva / day during ca. 1 month	Field & lab	–	(Schumacher 1910)
Nematinae	*Euura scutellata* (Hartig, 1837) (= *Pachynematus scutellatus*)	*Pentatoma rufipes*	Bug nymphs and adults often feeding on larvae; nymph V consume 0.35–0.8 sawfly larva / day	Field & lab		(Gäbler 1952)
Nematinae	*Pristiphora erichsonii* (Hartig, 1837)	*Picromerus bidens*, *Pinthaeus sanguinipes*	*P. bidens* associated with the sawfly 7 times, destroying an entire colony once; overall mortality <5%; last nymphal stage of *P. sanguinipes* associated with the sawfly 2 times	Field	–	(Pschorn-Walcher and Zinnert 1971)
Nematinae	*Pristiphora laricis* (Hartig, 1837) (= *Lagaeonematus laricis*)	"Bugs"	Moderate destruction of larvae by bugs	Field	–	(Hein 1956)
Nematinae	*Pristiphora laricis* (= *Lagaeonematus laricis*)	*Picromerus bidens*	"The bug mimics the larvae, as was observed on the tree"	Field	N/A	(Hsin 1935)
Selandriinae	*Aneugmenus padi* (Linné, 1760)	*Podisus maculiventris*	≥5O% Larvae killed and emptied after exposure to bug	Lab	–	(Boevé and Müller 2005)
Selandriinae	*Strongylogaster multifasciata* (Geoffroy, 1785), *Stromboceros delicatulus* (Fallén, 1808)	*Podisus maculiventris*	≥5O% Larvae alive or killed but not emptied after exposure to bug	Lab	+/–	(Boevé and Müller 2005)
Xyelidae						
Xyelinae	*Pleroneura* spp.	"Predaceous hemipteran"	Dried and shrivelled late-instar larvae occurred occasionally and may have been killed by bugs	Field	–?	(Ohmart and Dahlsten 1979)

The list is most probably not exhaustive. The authorship of the sawfly names follows the taxonomy in Taeger et al. (2010); a synonym is given between parentheses if used in the reference. Bug names have only been checked for their classification at family level. Their family name is mentioned between parentheses only for non-Pentatomidae. Original data were considered as far as possible, that is, data from secondary sources were generally not included. One reference (Hsin 1935) does not contain data about bugs preying on sawfly larvae, although cited for that reason by other references. The published data and observations are summarized in a brief one-sentence statement, and the sawfly defence is consequently judged as rather effective (+) or not (–). Not applicable (N/A).

[(1)] Species expected to contain toxic peptides, since these are present in congeneric species (Boevé et al. 2014, 2018b).

[(2)] Species not expected to contain toxic peptides, since these were not detected in two species from two different genera, *Perga* and *Pergagrapta*, but belonging to the same subfamily (Boevé et al. 2014).

[(3)] Species known to contain toxic peptides (Boevé et al. 2018b).

[(4)] The unidentified *Heteroperreyia* species mentioned in Mc Kay et al. (2019) corresponds to *H. kava* as described in Smith et al. (2019) (F. Mc Kay, personal communication, 2020).

[(5)] Species where toxic peptides were not detected (Boevé et al. 2014)

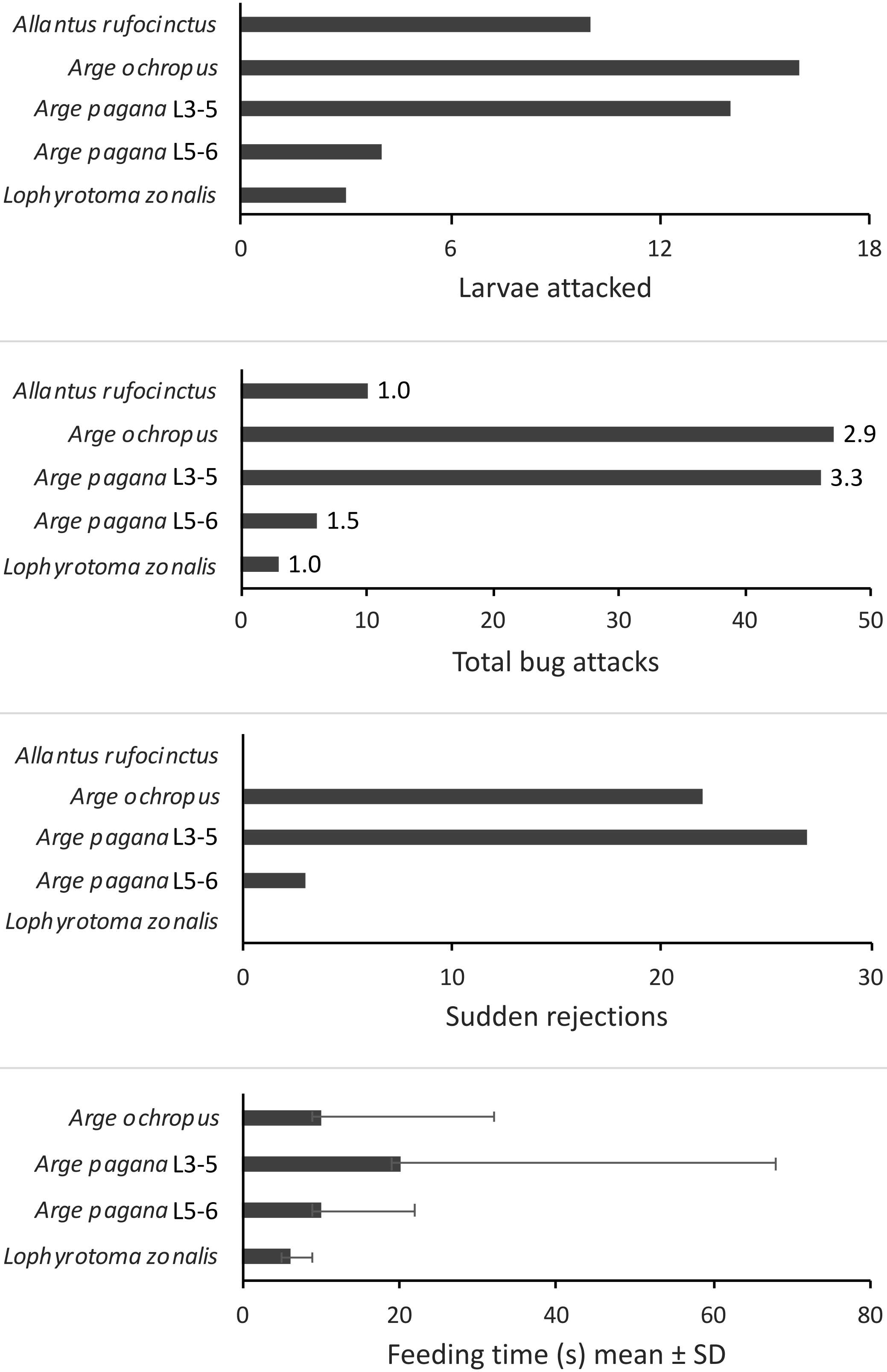
Table 2 Sawfly larvae used in the bioassays with *Picromerus bidens*, and part of the results

	Body length (mm)	**Larvae tested**	**Bug feeding time (s) mean ± SD [min. to max.]**	**Larvae alive at day 1/2/3**	**Bugs alive at day 3**
Allantus rufocinctus	21	18	– [56 to >1800]	0/0/0	18
Arge ochropus	20	18	10 ± 22 [1 to 128]	18/18/18	18
Arge pagana L3-5	14–18	18	20 ± 48 [1 to 300]	18/18/18	18
Arge pagana L5-6	18–20	18	10 ± 12 [1 to 35]	18/18/16	17
Lophyrotoma zonalis	23	18	6 ± 3 [2 to 10]	17/17/16	18

Data about body length are from Lorenz and Kraus (1957) and own observations, and the value for *L. zonalis* does not include the caudal appendage. Feeding times were measured from t = 0 to 30 min, and values given as mean ± standard deviation (SD) are also depicted in Fig. 1. (–) Not calculable. Sawfly and bug survival data were gathered following interactions from t = 0 to 24 h (i.e. day 1). See Fig. 1 for further results

Figure caption

Fig. 1 Results from bioassays with sawfly larvae offered to *Picromerus bidens*. Larvae were tested when full grown, *A. pagana* being also tested at younger instars (L3-5). Using 18 larvae per species/instar and tested singly against single bugs, the following measurements were gathered during 30 min of predator-prey interactions: the number of larvae attacked, the total number of attacks made by the 18 bugs, their total number of sudden rejections, and their feeding time. The values at the right of the “total bug attacks” histogram bars are the average number of bug’s feeding events per attacked larva. For more explanation, see text


Allantus rufocinctus
Arge ochropus
Arge pagana L3-5
Arge pagana L5-6
Lophyrotoma zonalis
0
6
12
18
Larvae attacked
Allantus rufocinctus
Arge ochropus
Arge pagana L3-5
Arge pagana L5-6
Lophyrotoma zonalis
1.0
2.9
3.3
1.5
1.0
0
10
20
30
40
50
Total bug attacks
Allantus rufocinctus
Arge ochropus
Arge pagana L3-5
Arge pagana L5-6
Lophyrotoma zonalis
0
10
20
30
Sudden rejections
Arge ochropus
Arge pagana L3-5
Arge pagana L5-6
Lophyrotoma zonalis
0
20
40
60
80
Feeding time (s) mean ± SD