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APPLICABILITY OF THE 'LOCOMOTOR GANGLIA' HYPOTHESIS TO THE STINGING BEHAVIOUR OF *SYMMORPHUS ALLOBROGUS*, A PREDATORY WASP HUNTING CHRYSOMELID LARVAE

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Abstract. *Symmorphus allobrogus* (Saussure) (Hymenoptera: Eumeninae) is a solitary wasp hunting the larvae of Chrysomelidae. Sting traces on 3,210 paralysed prey specimens were studied. In over 50% of the cases, the wasp directed 6–9 stings (average 8.7) to 4–6 (average 5.1) body segments of the prey. Usually stings were applied to the throat, thoracic segments, the first, and in almost half of the cases the second abdominal segment. The mobility of the prey was negatively correlated only with the stings directed to three thoracic and the first abdominal segments. Surprisingly, the prey stung on its throat remained more mobile than the prey not stung on it. Nearly 4% of the prey specimens were stung to their terminal abdominal segments, however, those stings had a little paralysing effect. Our data demonstrate that, with necessary adjustments, Steiner's (1986) 'locomotor ganglia' hypothesis may be applied to the stinging behaviour of *S. allobrogus*.

Key words: Chrysomelidae, Eumeninae, hunting, paralysis, reproductive behaviour, solitary wasp, Vespidae

INTRODUCTION

The ability to paralyse the host or prey by means of the ovipositor is one of the features of Apocrita that made possible the evolutionary success of this suborder of Hymenoptera. Studies into the interactions between stinging predators and their prey are important, because solitary wasps act as vital ecosystem agents, controlling populations of phytophagous insects, e.g. leafrollers (Jennings & Houseweart 1984; Collins & Jennings 1987; Harris 1994) and leaf beetles (Schenk & Bacher 2002).

Steiner (1986) has proposed five hypotheses concerning possible causal factors underlying stinging patterns in predatory wasps and has suggested that the 'locomotor ganglia' hypothesis is the most probable. According to this hypothesis, the wasp directs a sting for each nerve centre involved in a locomotion, attack or defence of the victim. This would imply that for most predatory wasps stings are directed to the throat (suboesophageal ganglion) and three thoracic segments of their prey. Steiner has abbreviated this basic stinging sequence as C4SP (a complete four-sting pattern). However, many wasps do not follow this rule.

Some wasp taxa that provision their offspring with a single large victim, such as Scoliidae, Tiphiidae, Pompilidae or Ampulicidae, may display a highly specialised stinging pattern and paralyse their victim by just one or two precisely directed stings (Malyshev 1966; Piek *et al.* 1984; Steiner 1986). The representatives of other wasp families that provision their nests with multiple small insects, also sting their prey only a few times or even once (Cooper 1953; Steiner 1976, 1979, 1983). However, wasps may sting multiple times if their prey is relatively large and has a weakly concentrated central nervous system (CNS) with multiple distinct ganglia, as in the cases of the sphecid wasp *Podalonia hirsuta* (Truc & Gervet 1984) or the eumenine wasp *Discoelius zonalis* (Veenendaal & Piek 1988).

Most wasps of the subfamily Eumeninae supply their offspring with the larvae of Lepidoptera; however, a few genera including *Symmorphus* capture the larvae of Coleoptera (Krombein 1964; Begum *et al.* 1991; Cowan 1991; Itino 1992; McCallan 1993). There are several studies devoted to the stinging pattern employed by eumenine predatory wasps while hunting caterpillars (Cooper 1953; Steiner 1983; Bonelli *et al.* 1980; Veenendaal & Piek 1988). However, the stinging pattern used by eumenines while hunting beetle larvae has not yet been described. Therefore, the aim of this study was to find out whether the stinging pattern of *Symmorphus allobrogus* (Saussure), an eumenine wasp hunting Chrysomelidae larvae, corresponds to the 'locomotor ganglia' hypothesis. For that purpose we tested the following three predictions:

(1) The main locomotor organs of chrysomelid larvae are thoracic legs and they use the abdomen with dorsal glands for defence (Pasteels *et al*. 1984; Dettner 1987; Dettner & Schwinger 1987; Vasconcellos-Neto & Jolivet 1994). On the other hand, chrysomelid larvae have a weakly concentrated CNS (Mason & Lawson 1981; Behura & Singh 1985). Hence, we predicted that, according to the 'locomotor ganglia' hypothesis, the stinging pattern of *S. allobrogus* should include stings directed to multiple segments of both thorax and abdomen. These stings may be more numerous than the basic C4SP.

(2) However, considering the size of the chrysomelid larva as prey, we supposed that it might be small enough to be stung just once or a few times to be paralysed.

(3) While some *Symmorphus* species, like the remaining eumenines, hunt caterpillars (Gathmann & Tscharntke 1999) other species of this genus, including *S. allobrogus*, are the only representatives of this subfamily provisioning their offspring with the larvae of Chrysomelinae leaf beetles (Fye 1965; Bonelli 1988; Cumming 1989; Hamanishi 1996; Sears *et al*. 2001; Budrienė 2003). Considering the Lepidoptera-hunting genera an outgroup, we regarded leaf beetle larvae as a derived type of prey within the genus *Symmorphus* in relation to caterpillars. Therefore, we tested the prediction that the stinging of an evolutionarily new prey may be not strictly specialised and may contain accidental or redundant stings with a little paralysing effect.

Material and methods

We studied the pattern of stung and non-stung segments and the distribution of sting traces among the segments of the paralysed prey specimens taken from fresh wasp nests. To assess the paralysing effect of stings, we analysed the dependence of prey mobility on the presence and the number of stings on different segments.

Research locality and material

Reed internode trap-nests were used to collect wasp nests. They were exposed on the walls of an old wooden house inhabited by the natural colonies of xylicolous solitary wasps in the locality of Varnupys, Lithuania (for detail: see Budrienė 2003). In total, we obtained 3,210 fresh prey specimens from 486 cells of 186 nests of *S. allobrogus* examined during 2000–2002. The studied prey consisted of the larvae of six Chrysomelinae species: *Linaeidea aenea* (Linnaeus), *Gonioctena quinquepunctata* (Fabricius), *G. viminalis* (Linnaeus), *Phratora laticollis* (Suffrian), *Plagiodera versicolora* (Laicharting), and *Gastrophysa viridula* (De Geer). At the current stage of research, we did not analyse differences between stinging patterns applied to different prey species.

Study of sting traces

Sting traces, visible as small, but distinct, rather uniform rounded or elliptic melanised scars, were counted on the paralysed prey larvae using a binocular microscope MBS-10 at a magnification of 32× to 56×. We found one prey individual without visible sting traces, which indicates that some stings might have been overlooked. It was also possible that in some cases the wasp might have stung the prey twice at the same point, thus leaving one scar only for more than one sting. Both possibilities mean that the actual number of stings delivered to the prey might have been slightly higher than the number of their traces observed. On the other hand, some scars might have had other origin than stinging; in such cases the number of wasp stings might have been lower than the number of scars. However, we supposed that the probability of such deviations was low and equal for each segment of prey, thus it did not bias substantially real stinging patterns.

After examination, we returned the prey larvae back into the nest cells, thus allowing the wasp larvae to develop to the adult stage for identification.

Study of the immobilising effect of stings

For the estimation of the paralysing effect of stings, we assessed the mobility of the intact prey, not yet damaged by the developing wasp larva.

The paralysed chrysomelid larvae responded to artificial stimulations such as prodding with a needle or grasping by movements of different intensity. As all the tests that checked the mobility of prey were carried out at approximately the same ambient temperature (22–25°C), we considered their results as fully comparable and dependent on the effect of paralysis only. Observations of the activity of 3,018 paralysed chrysomelid larvae enabled us to segregate the prey into four mobility classes: 0 – 'immobile': no discernible movements; 1 – 'less active': slow mouthpart or leg movements; body immobile; 2 – 'active': mouthparts or leg twitching, slow abdomen pulsations; and 3 – 'extremely active': mouthpart and leg twitching, slow head movements, pulsations of the neck, thorax, and abdomen, slow wriggling of the abdomen. In the quantitative analysis of our data, we used the above four mobility scores as a dependent variable that was negatively correlated with the depth of paralysis.

Statistical analysis

As the analysed variables (number of stings and prey mobility score) were taking values as relatively small integer numbers and were lacking the normal distribution, we analysed the data using the nonparametric statistics. To estimate the differences in the presence/absence of stings between any two segments of prey (the stinging probability), we used the Sign test. To assess the significance of the difference in the number of stings received by any two segments, we applied the Wilcoxon Matched-Pairs Signed-Ranks test. In order to compare the distributions of stings or stung segments with the expected distributions, we used the Chi-Square (χ^2) test. To assess the dependence of the number of stings directed to a particular segment of prey on the stings to other segments of prey and the dependence of the depth of paralysis on stings to particular segments, we used the Kendall Tau (τ) correlation analysis. These dependences were additionally verified by means of the Mann-Whitney U test, assessing the difference in the number of stings directed to various segments, as well as the mobility scores of the victims stung on the analysed segment and those not stung on it.

Statistical analysis was performed using the computer program StatSoft Statistica, release 6.0.

RESULTS

Stinging pattern

The wasp stung the chrysomelid larva predominantly from one (0.4% of the prey specimens) to 24 (0.2%) times. As an exception, single prey specimens had up to 136 sting traces and in the case of one studied prey larva no visible sting traces could be discovered. More than a half of all studied prey was stung six (10.6%), seven (14.0%), eight (14.4%), or nine (12.3%) times (Fig. 1). On average, a prey specimen received 8.72 ± 0.08 stings (here and hereinafter: mean ± SE; N = 3,210).

The distribution of stings among the anterior six body segments was highly variable and made a unique pattern in ca. 35% of the prey specimens. Commonly (45.2% of the prey) each of the six anterior segments received one sting, but often one or some of these segments were stung twice (21.3%) or were omitted without any sting (20.2%). Sometimes a segment received three (7.8%), four (3.1%), five (1.4%), six (0.5%) or over six (0.5%), and in a single case even up to 39 stings. Five anterior segments, from throat to first abdominal segment, were commonly stung once or twice, receiving on average about 1.5 stings per segment, while the average number of stings directed to the second abdominal segment was around 0.7 (Fig. 2). The distribution of stings delivered to the anterior five or six segments of prey differed significantly from a uniform distribution (χ^2 test, $P < 0.001$). The difference in the number of stings given to any two segments of prey was highly significant (Wilcoxon Matched-Pairs Signed-Ranks test, $P < 0.001$), except for the five pairs: throat–mesothorax, prothorax–metathorax, 6th–7th, 7th–8th, and 8th–9th abdominal segments.

The number of segments stung (including the throat) ranged from one to 11, the mode being five (Fig. 3). On average the number of stung segments was 5.08 ± 0.02. We found 230 different combinations of stung segments. Over 40% of the prey specimens were stung on their anterior five or six segments, while each of the other patterns comprised less than 6% of the total number of stinging patterns investigated.

The anterior five body segments of prey were stung with a probability higher than 80% (Fig. 4). The difference of stinging probability between any two segments was

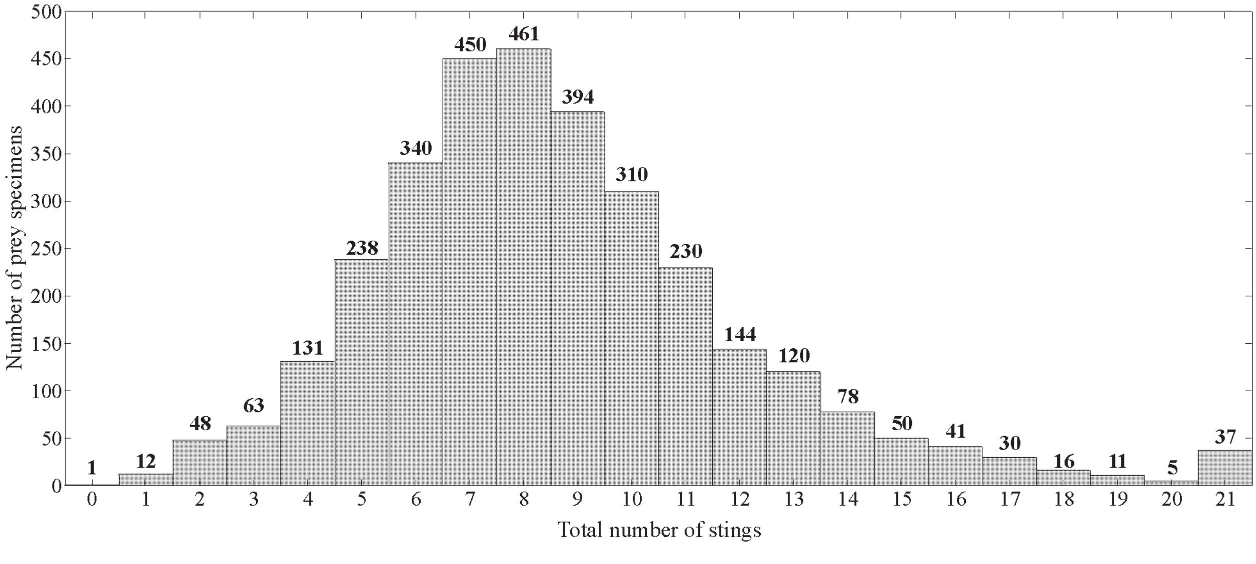

Figure 1. Prey of the predatory wasp *Symmorphus allobrogus*: total number of the received stings (N = 3,210).

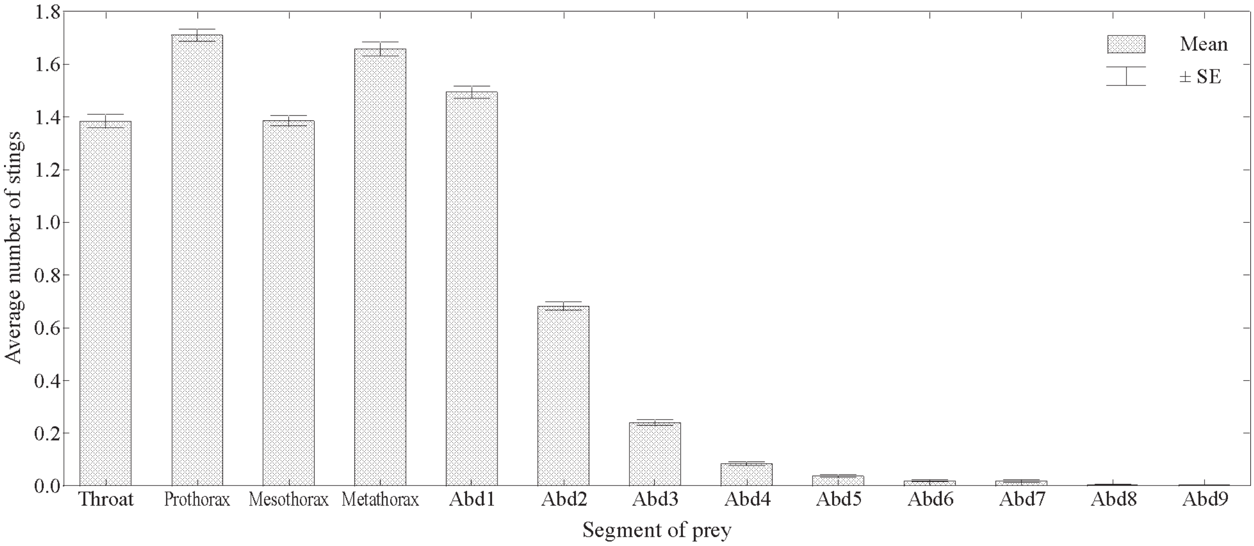

Figure 2. Average number of stings directed to prey body segments by the predatory wasp *Symmorphus allobrogus* (N = 3,210).

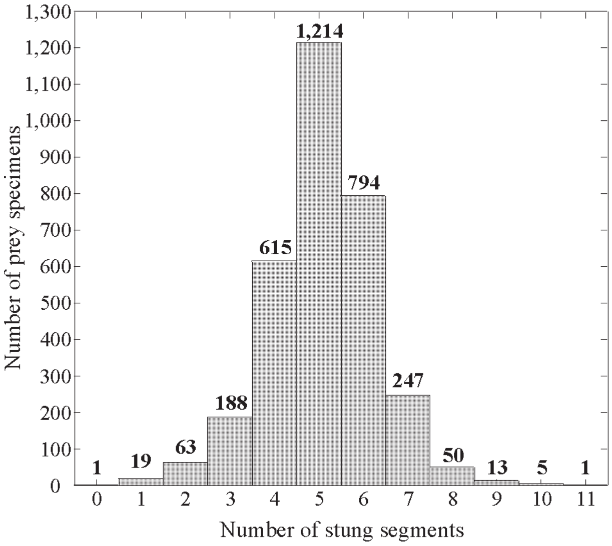

Figure 3. Prey of the predatory wasp *Symmorphus allobrogus*: number of stung body segments (N = 3,210).

significant (Sign test, $P < 0.001$), except for the following six pairs: throat–first abdominal segment, prothorax–metathorax, mesothorax–first abdominal segment, 6th–7th, 7th–8th, and 8th–9th abdominal segments. The distribution of the observed stinging probabilities among the segments of prey was significantly different (χ^2 test, $P < 0.001$) from the expected uniform distribution resulting from equal probabilities of stinging of each of the anterior five or six segments.

Interdependence of stinging on different segments

In order to determine whether the stinging effort of the wasp directed to a particular prey segment was dependent on the amount of stinging directed to other segments, we calculated Kendall τ correlation of the presence and the number of sting traces between each pair of segments. Significance of the revealed regularities was additionally tested and confirmed by means of the Mann-Whitney U test.

The results of the above analysis (Table 1) revealed five weak, but significant regularities: (a) a positive correlation of the presence and the number of stings between all neighbouring segments of prey, except the pair throat–prothorax. That correlation was stronger for the thoracic and the mid-abdominal segments; (b) negative correlation between the number of stings on the throat and on the first, second, and sixth abdominal segments; (c) positive correlation between the number of stings on the pro- and mesothorax and on the terminal abdominal segments; (d) negative correlation between the number of stings on the metathorax and on the second–fourth abdominal segments; and (e) positive correlation between the presence of stings on the subbasal (second–fourth) and on the terminal (sixth–ninth) abdominal segments.

Dependence of paralysis on the stinging pattern

The prey larvae were classified by their mobility as follows: 1,393 as ‘quiet’ (mobility score 0), 683 as ‘less active’ (1), 693 as ‘active’ (2), and 249 as ‘extremely active’ (3). The mean value of the mobility score of all the studied prey was 0.93 ± 0.02 (N = 3,018).

The prey was more deeply paralysed as a result of both a higher total number of stings (correlation between the mobility score and the number of stings: $\tau = -0.165$, $P < 0.001$) and a higher number of stung segments ($\tau = -0.052$, $P < 0.002$).

We separately analysed the mobility of the prey stung on a certain number of segments and the prey that received a certain total number of stings. The analysis

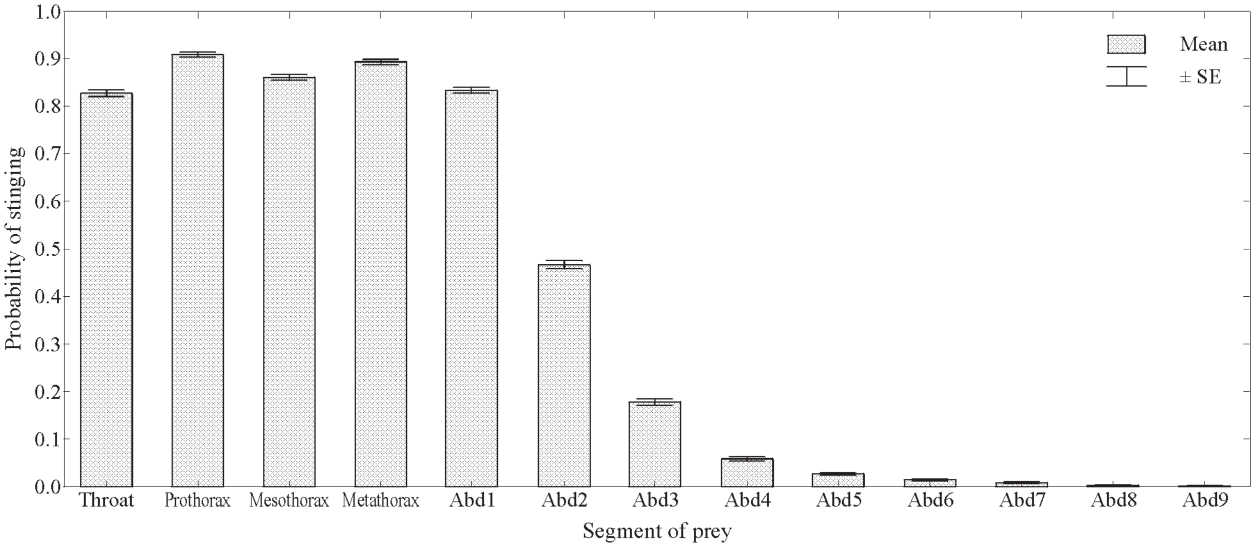

Figure 4. Probability of stinging different prey body segments by the predatory wasp *Symmorphus allobrogus* (N = 3,210).

Table 1. Correlation (Kendall τ values) of the presence (the lower left part of the table) and number of stings (the upper right part of the table) directed to various segments of prey. Only significant ($P < 0.05$) τ values are presented; highly significant values ($P < 0.001$) are shown in bold; N = 3,210.

Prey segments	Throat	Pro-thorax	Meso-thorax	Meta-thorax	Abd.1	Abd.2	Abd.3	Abd.4	Abd.5	Abd.6	Abd.7	Abd.8	Abd.9
Throat			**0.09**	0.03	**-0.05**	-0.03				**-0.04**			
Prothorax			**0.19**	**0.13**	**0.05**				0.03	**0.06**	0.03	**0.06**	0.03
Mesothorax		**0.17**		**0.18**	**0.07**		0.03		0.02	**0.04**	0.03	0.04	
Metathorax		**0.11**	**0.21**		**0.12**	**-0.05**	**-0.06**	-0.02					
Abd.1		**0.06**	**0.09**	**0.09**		**0.05**	-0.02						
Abd.2	-0.02				**0.10**		**0.18**	**0.09**	**0.04**	0.02		**0.04**	
Abd.3						**0.19**		**0.22**	**0.14**	**0.06**	**0.06**		**0.04**
Abd.4				-0.03	-0.02	**0.08**	**0.21**		**0.20**	**0.14**	**0.05**		0.03
Abd.5	-0.04				0.03	0.03	**0.14**	**0.20**		**0.40**	**0.27**	**0.10**	**0.04**
Abd.6	**-0.04**		0.03				**0.05**	**0.14**	**0.40**		**0.33**	**0.09**	**0.13**
Abd.7	-0.03				0.02		**0.06**	**0.05**	**0.27**	**0.33**		**0.12**	**0.17**
Abd.8						**0.05**			**0.09**	**0.09**	**0.12**		**0.14**
Abd.9							**0.04**	0.02	**0.04**	**0.13**	**0.17**	**0.14**	

revealed that if the number of stung segments was higher than two, the mobility was always negatively correlated with the total number of stings (Table 2: columns). In contrast, the correlation between the mobility and the number of stung segments of the prey that received a particular total number of stings was negative only for the specimens stung just two or three times; for those having more sting traces it was positive or not significant (Table 2: rows).

The comparison of the mean mobility scores of the prey that received a particular number of stings on each of the anterior seven body segments demonstrated that generally the mobility decreased with the increasing number of stings on these segments (Fig. 5). However, this dependence was obvious only for three thoracic and the first abdominal segments. In contrast, the prey specimens stung once to the throat or to the second or third abdominal segment were on average significantly more mobile than the prey not stung on that segment.

The analysis revealed a highly significant ($P < 0.001$) negative correlation between the mobility score of prey and both the presence and the number of sting traces on three thoracic segments and the first abdominal segment (Table 3). The mean mobility score of the prey stung on

Table 2. Average mobility score of the prey (brackets: N) and the correlation of mobility with the number of stung segments and the total number of stings received. Only significant ($P < 0.05$) τ values are presented; highly significant values ($P < 0.001$) shown in bold.

	Number of stung segments										τ*
Total number of stings received	1	2	3	4	5	6	7	8	9	10	
1	1.91 (11)										
2	2.33 (6)	1.50 (38)									-0.27
3		2.17 (6)	1.54 (52)								-0.17
4		2.33 (6)	1.21 (42)	1.17 (72)							
5		2.67 (3)	1.06 (36)	1.26 (95)	1.28 (94)						
6		1 (1)	0.67 (15)	0.95 (104)	1.16 (141)	1.11 (57)					0.09
7		3 (1)	1.55 (11)	0.87 (84)	0.97 (203)	1.02 (100)	1.67 (15)				
8			0.75 (12)	0.77 (73)	0.94 (198)	1.11 (121)	1.20 (25)	2.00 (4)			**0.13**
9			2 (3)	0.89 (61)	0.73 (168)	0.82 (98)	0.91 (33)	1 (1)	2 (1)		
10	0 (1)		0 (1)	0.56 (27)	0.64 (123)	0.90 (105)	1.03 (31)	1.25 (4)			**0.17**
11				0.63 (16)	0.60 (72)	0.59 (87)	0.66 (35)	0.86 (7)	1 (1)		
12				0.67 (15)	0.56 (48)	0.72 (50)	0.70 (20)	0.67 (3)			
13			0 (2)	1.20 (10)	0.50 (38)	0.53 (38)	1.00 (21)	1.00 (4)	1.33 (3)	1 (1)	0.14
14			0 (1)	0.57 (7)	0.39 (18)	0.72 (32)	1.00 (11)	1.20 (5)	1 (1)	1 (1)	0.22
15				1 (4)	0.58 (12)	0.81 (16)	1.14 (14)	1.00 (3)	0 (1)		
>15		0 (1)	0 (2)	1 (7)	0.65 (26)	0.64 (44)	0.75 (32)	0.59 (17)	1.40 (5)	1.00 (3)	
τ**		0.25	**-0.20**	**-0.13**	**-0.19**	**-0.15**	-0.13	-0.27			

** – Kendall Tau correlation (τ values) between the mobility and the number of stung segments calculated for the prey with a given total number of stings (rows)*

*** – Kendall Tau correlation (τ values) between the mobility and the total number of stings calculated for the prey with a given number of stung segments (columns)*

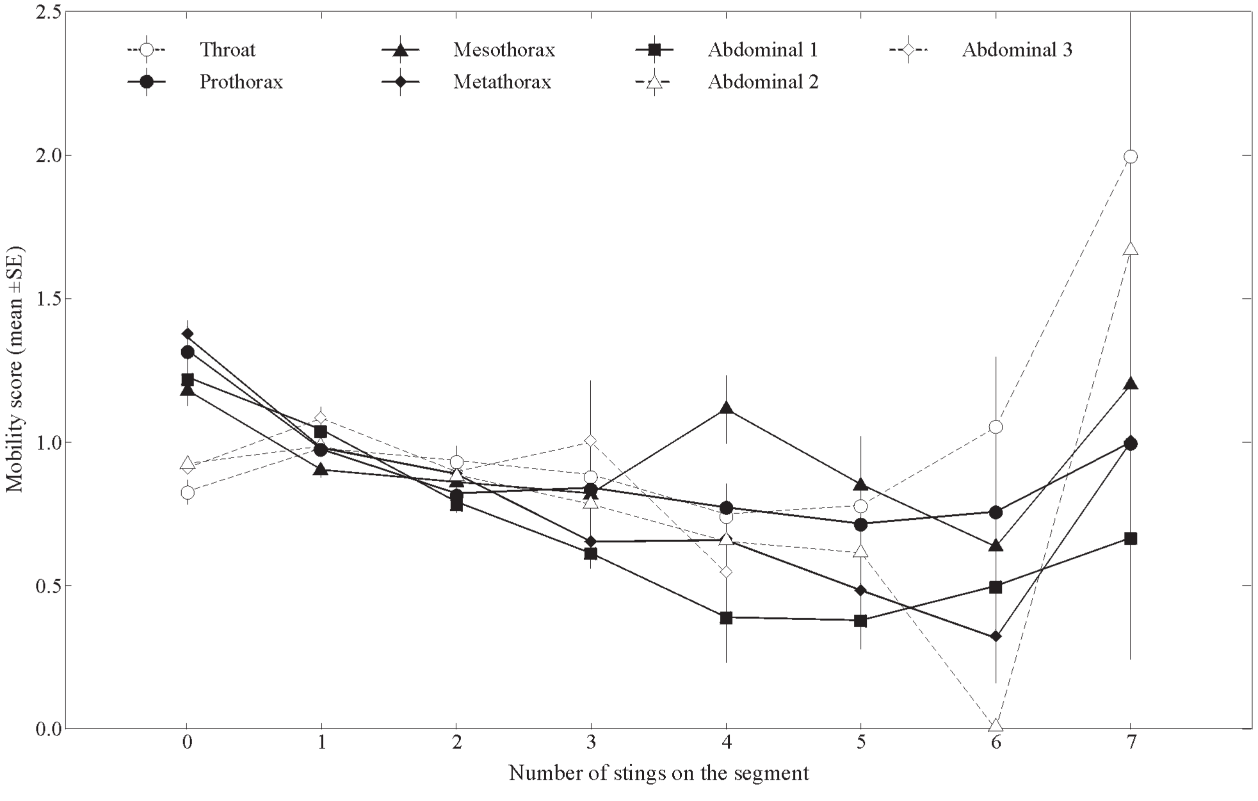

Figure 5. Prey of *Symmorphus allobrogus*: dependence of the average mobility score on the number of stings directed to the throat, thoracic and the first three abdominal segments (total N = 3,210 for each of the seven series).

Table 3. Difference in mobility between the prey specimens stung and not stung on certain body segments, and the dependence of their mobility on the presence and the number of stings on those segments. Only significant ($P < 0.05$) Z and τ values are presented in the table. Highly significant values ($P < 0.001$) are shown in bold; N = 3,018.

	Mean mobility score of the prey (brackets: N)		Difference in mobility between the prey stung and not stung on the segment: U test		Correlation (Kendall τ values) between the mobility score and	
	not stung on the segment	stung on the segment	Z	P	the presence of stings	the number of stings
Throat	0.83 (507)	0.95 (2,511)	-2.47	<0.01	**0.045**	
Prothorax	1.32 (270)	0.89 (2,748)	**5.91**	<0.001	**-0.107**	**-0.106**
Mesothorax	1.18 (421)	0.89 (2,597)	**4.71**	<0.001	**-0.085**	**-0.060**
Metathorax	1.37 (315)	0.88 (2,703)	**7.61**	<0.001	**-0.138**	**-0.160**
Abd.1	1.23 (504)	0.87 (2,514)	**6.57**	<0.001	**-0.119**	**-0.194**
Abd.2	0.93 (1,611)	0.94 (1,407)				
Abd.3	0.91 (2,473)	1.04 (545)	-2.97	<0.005	**0.054**	**0.049**
Abd.4	0.93 (2,842)	0.95 (176)				
Abd.5	0.93 (2,939)	0.97 (79)				
Abd.6	0.93 (2,975)	1.07 (43)				
Abd.7	0.93 (2,990)	1.29 (28)	-1.99	<0.05	0.036	0.036
Abd.8	0.93 (3,008)	1.50 (10)			0.030	0.030
Abd.9	0.93 (3,013)	1.80 (5)			0.034	0.034

any of these segments was significantly lower than that of the prey not stung on the corresponding segments (Mann-Whitney U test: $P < 0.001$). Therefore we may consider three thoracic segments and the first abdominal segment of the chrysomelid larva as segments containing the ‘locomotor ganglia’ in the sense of Steiner (1986).

In contrast, the mobility of prey was positively correlated with the presence and/or the number of stings on the throat, the third abdominal segment, and terminal abdominal segments; these findings were confirmed by the U test (Table 3).

Additionally, we assessed the combined paralysing effect of stings directed to different segments. The highest paralysing effect was observed in relation to stings on all four ‘locomotor’ segments (mean mobility score 0.80 ± 0.02, N = 1,912), as well as to stings on the prothorax, metathorax, and the first abdominal segment (0.81 ± 0.02, N = 2,114). A few prey specimens not stung on any of these segments preserved the highest mobility (2.25 ± 0.28, N = 12, and 2.33 ± 0.23, N = 15, respectively).

The prey with a higher combined number of sting traces on the pro- and mesothorax than on its metathorax and the first abdominal segment was significantly more active (mean mobility score 1.04 ± 0.03, N = 1,107) in comparison with the prey having more sting traces on its metathorax and the first abdominal segment than on its pro- and mesothorax (mean mobility score 0.87 ± 0.02, N = 1,911; Mann-Whitney U test: $P < 0.002$). Thus these data demonstrate the importance of stings directed to the metathorax and the first abdominal segment for the paralysis of Chrysomelidae larvae.

DISCUSSION

Stinging pattern

Nearly 70% of the studied prey was stung on all thoracic segments, and only 1% of the prey was not stung on any of these segments. In addition to this, the stings on the first abdominal segment were typical, too, and the stings on the second abdominal segment were applied to almost a half of the victims (Figs 2, 4). Stings directed to the third and fourth abdominal segments were less common (21% of the prey), but also not exceptional. These data support our first prediction (see Introduction).

In over 52% of the cases, the stinging pattern of *S. allobrogus* consisted of six to nine stings directed to five or six anterior segments of prey: the throat, three thoracic segments, and one or two basal abdominal segments. This number of stings cannot be considered as small; therefore our second prediction must be rejected.

Following Steiner (1986), we may abbreviate the most common stinging pattern of *S. allobrogus* as C5SP (a complete five-sting pattern).

The analysis of correlations between the stings directed to different segments of prey (Table 1) demonstrated that the wasp tended to sting the neighbouring segments (regularity (a) – see Results). It is likely that this rule reflects a relic of the serial 'segment-by-segment' scenario of stinging behaviour, inherited from the ancestors that hunted prey with a weakly concentrated CNS, containing multiple segmental ganglia. However, for the prey stung 6, 8, 10, 13 and 14 times, the efficiency of paralysis significantly decreased, when the stings were scattered among a larger number of body segments (Table 2). On the other hand, the number of stung segments of the chrysomelid larva was restricted to four, five or six in more than 80% of the specimens.

We may note a peculiar symmetry in the distribution of the amount of stinging directed by *S. allobrogus* to the anterior and posterior 'locomotor' segments of prey: the amount of stinging directed to the pairs of segments prothorax–mesothorax and metathorax–first abdominal segment is approximately equal (Figs 2 and 4). Interestingly, Steiner (1983) has emphasised that in *Euodynerus foraminatus*, a species employing a two-sting pattern, a roughly equal amount of stings is directed to the throat–prothorax and the mesothorax–metathorax of its caterpillar prey. Hence, the symmetry of the distribution of stings described by us in *S. allobrogus* may be inherited from the caterpillar-hunting ancestors of this species that had a two-sting pattern, as *A. antilope* and *E. foraminatus*, and it may be related to the suggestion that the C5SP of *S. allobrogus* was secondarily augmented and 'despecialised', when these wasps started to capture an evolutionarily new type of prey, the leaf beetle larva.

Nearly 4% of the studied victims were stung on their terminal (5th–9th) abdominal segments. We suggest that the wasp applies additional stings to these segments in the case of chrysomelid larvae, which are very wriggly and difficult to paralyse as they vigorously defend themselves by the movements of their abdomen. This suggestion is supported by a higher mobility of the prey stung on the above segments, as well as by a positive correlation between the mobility and the presence of stings on these segments (Table 3). Additional stinging on the abdomen occurring solely in the case of unusually active prey specimens explains strong correlation of the presence and the number of stings between the neighbouring abdominal segments (Table 1).

A negative correlation between the number of stings on the metathorax–first abdominal segment and the stings on the second–fourth abdominal segments (regularity (d); Table 1) might imply that the wasp sometimes misses a segment, while stinging posterior 'locomotor' segments and delivers a part of stings to subsequent abdominal segments. Stinging of the latter segments may have a lesser paralysing effect than well-directed stings on the metathorax and the first abdominal segment. A possible result of such 'mistakes' is a positive correlation between the mobility of prey and the presence and the number of stings on the third abdominal segment (Table 3).

Another result of such stinging 'mistakes' might be a positive correlation between the presence and the number of stings on the terminal (sixth–ninth) abdominal segments and the stings on the third–fourth abdominal segments (regularity (e); Table 1): a higher activity of the prey specimens stung on the latter segments instead of the metathorax and the first abdominal segment possibly stimulated the wasp to sting the former segments.

Our results revealed a high intra-populational variability of the stinging pattern of the predatory wasp *S. allobrogus* (Figs 1 and 3), demonstrating that the stinging behaviour of this species is far from being stereotypical or specialised. Thus, our third prediction (see Introduction) may be credible. Some of the observed variability might have been caused by inaccuracy of the method (study of scars instead of the direct documentation of stinging behaviour of the wasp). However, we expected that a large number of observations compensated this possible inaccuracy.

Immobilising effect of the stings

An increasing total number of stings decreased the mobility of prey with three or more stung body segments (Table 2: columns). However, the comparison of the prey larvae, which received an equal number of stings, but on a different number of segments, revealed that stings caused a deeper paralysis when they were concentrated on a lesser number of segments (Table 2: rows). The exceptions were the prey stung only twice or thrice: in these specimens the stings ensured a better paralysis when they were more scattered.

Only the stings on three thoracic and the first abdominal segments had a major paralysing effect, decreasing significantly the mobility of prey (Table 3, Fig. 5). Therefore, when applying the 'locomotor ganglia' hypothesis to the chrysomelid larva, we may only consider these four segments as containing the 'locomotor ganglia'. Stings on the metathorax and the first abdominal segment seemed to be of particular importance, as the prey stung on these two segments had the lowest mean mobility.

The revealed lesser paralysing efficiency of stings on the anterior 'locomotor' segments, in comparison with the posterior ones, might explain the positive correlation between the stinging on the pro- and mesothorax, and the stinging on the terminal abdominal segments (regularity (c); Table 1): additional stings on the abdomen could be stimulated by a higher activity of prey specimens that were less strongly immobilised by stinging on their anterior 'locomotor' segments.

Surprisingly, the stings directed to the throat did not decrease general mobility of prey. Quite the opposite, the larvae stung once on their throat seemed to be even more mobile than those not stung on it (Fig. 5). This rule was confirmed by a positive correlation between the mobility score of prey and the presence of stings on the throat, as well as a significantly higher mean mobility of the chrysomelid larvae stung on the throat (Table 3). The stings directed to the suboesophageal ganglion are known to play an essential role in deactivation of prey when the paralysis is transient or imperfect (Steiner 1983; Piek *et al*. 1984). As Gnatzy (2001) has revealed, although the sting directed to the suboesophageal ganglion can suppress spontaneous behaviour, it is not compellingly necessary for the generation of long-term effects. Therefore, we suppose that the stings directed to the throat of the chrysomelid larva may cause a transient (reversible) deactivating effect, which reduces the number of effective immobilising stings stimulated to a certain extent by the activity of prey. After recovering from this temporary paralysis, the prey may finally remain more mobile than the one not stung on its throat. This suggestion is supported by a negative correlation between the presence of stings on the throat and abdominal segments (regularity (b); Table 1). Since additional stings on the abdomen were given to particularly reactive prey, a temporary paralysis caused by stinging of its throat decreased the number of these stings.

The optional stings on the terminal abdominal segments were not typical of the stinging pattern of *S. allobrogus* and had a weak effect, as the prey that received them retained a comparatively high mobility level (Table 3). However, they demonstrate flexibility of the stinging behaviour that allows the switching of the predator to new types of prey and the evolutionary process of 'search' for prey's segments and ganglia, stings on which may ensure an efficient paralysis.

Applicability of the 'locomotor ganglia' hypothesis

We conclude that the stinging pattern of *S. allobrogus* commonly consists of one or two stings directed to the throat (suboesophageal ganglion), probably providing a transient immobilisation, and four to eight main paralysing stings directed to thoracic segments, and one or two basal abdominal segments. Occasionally the stinging pattern includes stings on sub-basal (third–fourth) abdominal segments, which actually may be misdirected stings that should have been delivered to basal (first–second) abdominal segments. A particularly active chrysomelid larva may receive some additional stings on terminal (5th–9th) abdominal segments.

Results of our study generally confirm that Steiner's 'locomotor ganglia' hypothesis may be applied to *S. allobrogus*. Our data adjust this hypothesis for the chrysomelid larva as prey (1) by revealing that the stings directed to the throat do not have a final paralysing effect, and (2) by demonstrating that the stings directed to the first abdominal segment have as high importance for paralysis as those directed to thoracic segments.

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„LOKOMOTORINIŲ GANGLIJŲ“ HIPOTEZĖS TAIKYMAS VAPSVAI-ENTOMOFAGEI *SYMMORPHUS ALLOBROGUS*, MEDŽIOJANČIAI LAPGRAUŽIŲ LERVAS

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SANTRAUKA

Symmorphus allobrogus (Saussure) (Hymenoptera: Eumeninae) yra pavieniui gyvenanti vapsva, medžiojanti vabalų-lapgraužių (Chrysomelidae) lervas. Buvo ištirti įgėlimų pėdsakai ant 3210 paralyžiuotų grobio individų iš šviežių vapsvų lizdų, padarytų dirbtinėse lizdavietėse. Daugiau nei 50% atvejų vapsva gėlė lapgraužio lervą 6–9 kartus (vidurkis 8,7) į 4–6 (vidurkis 5,1) jos kūno segmentus. Paprastai įgėlimai buvo nukreipiami į galvos apatinę dalį, tris krūtinės segmentus, pirmąjį pilvelio segmentą ir beveik kas antram grobiui į antrąjį pilvelio segmentą. Paralyžiuoto grobio judrumo laipsnis neigiamai koreliavo su įgėlimų į tris krūtinės segmentus ir pirmąjį pilvelio segmentą skaičiumi. Įdomu, kad grobis, įgeltas į apatinę galvos dalį (poryklinį ganglijų) buvo judresnis, negu grobis, neįgeltas į ją. Beveik 4% grobio individų buvo įgelti į jų pilvelių galo segmentus, tačiau šie įgėlimai neturėjo pastebimo paralyžiuojančio poveikio. Mūsų duomenys rodo, kad „lokomotorinių ganglijų“ hipotezė su atitinkamais patikslinimais gali būti taikoma vapsvos *S. allobrogus* gėlimo elgsenai.

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