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Adaptability of prey handling effort in relation to prey size in predatory wasps (Hymenoptera: Eumeninae)

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The stinging pattern of a predatory wasp is a behavioural trait, affecting the possible evolutionary changes of its niche, e.g. widening or shifting the prey spectrum. We tested the hypothesis that the ability of a predator to adjust its handling effort to the size of prey is a species-specific trait, the parameters of which depend on the size and size range of the exploited prey. We found that wasps better adjust their stinging effort to prey size if they hunt relatively larger or relatively more variable prey. This adaptability differs amongst neighbouring phylogenetic lineages. We presume that evolution of prey-handling behaviour may result in two types of tactics: the first, an application of precise techniques for optimal prey immobilization, little dependent on prey size and typical of specialists. The second tactic typical of generalists is a less precise handling, causing more general damage to the prey with an intensity dependent on its size.

Introduction

Optimal foraging theory refers to several trade-offs made in relation to the energy content of prey (Pyke *et al*. 1977). Generally, prey profitability is defined as the rate of energy gain against the associated hunting effort (MacArthur & Pianka 1966). The latter includes the searching effort, handling effort (including capture, subduing and assimilation) and, for central-place predators, transfer effort. The searching and transfer efforts needed to consume a specific prey are mostly affected by ecosystem characteristics, such as the density and distribution of prey populations, the suitability of the habitat for both predator and prey and the availability and distribution of nesting sites for the central place predator. In contrast, the prey handling effort is defined by the predator's characteristics, such as the trophic niche and species-specific behavioural traits. We may expect that specialist predators are able to handle individuals of their favourite prey species faster, or with relatively lesser effort, and assimilate them more efficiently than prey of any other species.

Since a specialist predator is adapted to exploit either a single or a few ecologically and chemically similar prey species, that differ little in their detectability and assimilation rate, the choice of the optimal size of prey may be a critical decision in its foraging behaviour. The consumption of large prey results in a high energy intake. However, if the prey is relatively too large, the associated handling effort may become inordinately high as well (Aljetlawi *et al*. 2004). Relatively small prey specimens might be preferred due to a considerably higher success rate of the attacks (Cogni *et al*. 2002).

The energy intake/handling effort rate may have a hump-shaped dependence on prey size (Persson *et al*. 1998), the slopes of this dependence created on the one side by an unreasonably high handling effort for large prey specimens and on the other by a too low energetic value of small prey, which still requires some minimum of handling. We may assume that an evolutionary widening or shift of prey size range is achievable through the widening of the middle part of this hump-shaped dependence in both directions. The behaviour of a specialist predatory species may be directed by selection towards the polishing of highly efficient subduing techniques, which with the same effort could be applicable to larger potential prey specimens of a particular type. This evolutionary pathway would lead to the adaptation of handling behaviour to the morpho-physiological traits of a narrower range of prey taxa. The result of evolutionary changes to maximise beneficial exploitation of smaller prey specimens is a higher adaptability of handling effort, i.e. an ability to simplify and reduce it while subduing smaller prey specimens, thus always maintaining a profitable energy intake-handling effort rate.

In this research, we focused on the hunting behaviour of Eumeninae predatory wasps, namely representatives of the genera *Ancistrocerus*, *Discoelius* and *Symmorphus*. These insects are solitary mass-provisioners, building multicellular linear nests in pre-existing cavities. They are central-place predators, provisioning each brood cell of their nests with multiple paralysed caterpillars or beetle larvae (Krombein 1967, Cowan 1991, Itino 1992, 1997, McCallan 1993). At the species level, eumenines are oligophagous or almost monophagous specialists, hunting prey of a single or a few related families, a single subfamily, or even a single genus (Sears *et al*. 2001, Budriene 2003). At the genus level, however, the studied taxa have a prey range of different widths: *Ancistrocerus* always hunt caterpillars of several leaf-rolling “Microlepidoptera” families, while the other two genera exploit a wider range of prey belonging to more than one insect order. *Discoelius* wasps hunt caterpillars of multiple moth families as well as sawflies (Lepidoptera and Hymenoptera); most *Symmorphus* species prey on larvae of leaf beetles, weevils (Coleoptera: Chrysomelidae and Curculionidae) and caterpillars (Lepidoptera) (Gathmann & Tscharntke 1999, Rodrigues da Silva & Jaffe 2002, Budriene 2003).

As with most predatory wasps, the prey handling behaviour of the studied species includes stinging, an element that may be roughly quantified by the number of stings delivered to a victim. The injected venom may have complicated ethological and physiological consequences for the victim (Libersat 2003, Haspel *et al*. 2005). In most solitary wasps, the venom partially paralyses the central nervous system, immobilising the prey but not killing it (Gnatzy 2001). We, therefore, assume that the stinging pattern and stinging effort applied to the individual prey is a critical species trait in stinging wasps, ensuring the survival of their offspring. In addition to higher physiological costs of venom synthesis for the wasp, a too high stinging effort may result in the death of the prey, which may then dry out and become inedible for the wasp larva. In the event of an inadequate stinging pattern or a too low stinging effort, an active prey may damage the young wasp larva, or in the case of larval prey, may develop to a pupa or even imago inside the brood cell, thus also becoming inedible (own unpubl. data).

Since the studies of Fabre (1879–1910), the stinging of prey by a predatory wasp has been considered an inherited behavioural sequence, a strictly fixed set of stings ensuring the injection of paralysing venom to the major “locomotor” ganglia of victim’s central nervous system (Evans 1966, Steiner 1986), which presumably does not depend on the size of the victim. The “ancestral” stinging wasps, which use a single large prey to provision their offspring (i.e., Scoliidae, Tiphiidae, Pompilidae, Ampulicidae), may paralyse their prey by just one or two precisely aimed stings (Malyshev 1966, Piek *et al*. 1984, Libersat *et al*. 1999). In several studied Crabronidae wasps, such a fixed stinging sequence is known as a “complete four-sting pattern” (C4SP), including stings to the throat and three thoracic segments (Steiner 1986, Gnatzy 2001).

In Eumeninae wasps, two general types of stinging pattern have been described. Representatives of the caterpillar-hunting genus *Ancistrocerus* apply a more or less stable "complete two-sting pattern" (C2SP), delivering one sting to the suboesophageal or prothoracic ganglion and the second sting to the metathoracic ganglion of the victim (Steiner 1983, Budriene & Budrys 2005a). The caterpillar-hunting *Discoelius* and mostly beetle larva-hunting *Symmorphus* deliver stings to the throat, the thoracic segments, and one or several abdominal segments of their victim (Veendaal & Piek 1988, Budriene & Budrys 2005a). *Symmorphus allobrogus*, for instance, applies a five-sting pattern (Budriene & Budrys 2004). The total number of delivered stings significantly positively depends on the size of prey, implying that predatory wasps have adaptable handling behaviour; this adaptability is better expressed in *Discoelius* and *Symmorphus*, but it is weak in *Ancistrocerus* (fig. 1 in Budriene & Budrys 2005b). However, the relative stinging effort (stings per prey weight unit) negatively depends on the prey size (fig. 2 in Budriene & Budrys 2005b), meaning that wasps have a certain minimum limit of stinging effort, which must be applied to paralyse their victim, even if it is small. Therefore, we presume that the stinging pattern of predatory wasps may include a fixed minimal set of stings, directed to the most important ganglia of the prey (C4SP, C2SP, etc.) and a flexible number of additional stings, which depend on the size and resistance ability of the prey. This flexible part of the stinging pattern also provides a pool for evolutionary changes of stinging behaviour in cases of a widening or shift in the prey range.

In this study, we intended to investigate how the size and the variability of size of the hunted prey is affected by the body size of the eumenine wasps. We then tested a hypothesis that the ability to adjust the handling effort to the size of prey is the predator's species-specific behavioural trait, parameters of which depend on the relative size and the size range of the exploited prey.

Material and methods

Predators and their prey

We studied the stinging pattern of twelve cavity-nesting predatory wasp species (Hymenoptera: Vespidae: Eumeninae), whose prey could be obtained in large numbers by applying reed stem trap-nests. Five of the studied species, *Symmorphus allobrogus*, *S. angustatus*, *S. bifasciatus*, *S. crassicornis* and *S. murarius*, supply their offspring with larvae of Chrysomelinae leaf beetles. The other seven species, *Ancistrocerus antilope*, *A. claripennis*, *A. nigricornis*, *A. trifasciatus*, *Discoelius dufourii*, *D. zonalis* and *Symmorphus debilitatus*, provision their larvae mostly with lepidopteran caterpillars.

In captivity, three species (*S. allobrogus*, *S. bifasciatus* and *S. crassicornis*) presented a stinging behaviour similar to the one observed in the natural environment. A female wasp spent approximately 10 minutes handling a single prey specimen. In the observed cases of stinging, the female wasp moved the tip of its abdomen along the cuticle of prey in tight contact, so that single insertions of the sting were not visible. The number of delivered stings could be established a few hours later by counting sting traces, easily visible at 32× to 63× magnification as small but distinct, rather uniform, ovoid or elliptic melanised scars on the cuticle of prey. After obtaining experience in counting scars on the prey stung in captivity, we studied the stinging patterns on prey specimens hunted in the wild, retrieving them from fresh wasp brood cells made in the trap nests. We considered the number of sting traces to be the best available parameter to reflect the stinging effort of a female wasp. Body weight was regarded as the most appropriate parameter to reflect the energetic profitability of the prey.

Collection of material

We collected the material during the years 2002 to 2006 at the following localities of Lithuania: Bilšiai (55°08´N, 25°16´E), Papiškiai (55°56´N, 24°16´E), Taraldžiai (55°46´N, 25°22'E) and Varnupys (55°24´N, 25°17'E). Wasp nests were obtained using bundles of 25–35 internode fragments of reed (*Phragmites australis*) stems as trap-nests. These were placed on the outer walls of old buildings with natural colonies of the cavity-nesting solitary wasps. The construction of two types of the used trap-nests is described by Budriene (2003) and Budrys *et al*. (2010).

During the summer seasons, the stem internodes containing freshly completed wasp nests with visible external plugs were regularly taken from the trap nests. They were then dissected and the paralysed prey specimens, as yet undamaged by the developing wasp larva, were taken from the brood cells. Each prey specimen was weighed to the nearest 0.1 mg and the sting traces on it were counted. A total of 5726 fresh prey specimens from 443 wasp nests were analysed.

After examination, the prey specimens were returned back to the brood cell, the nests were closed and stored. At the end of the season, the diapausing prepupae of the wasps were reactivated in a refrigerator (+4 °C), allowing them to develop to imagoes in order to identify the species. The emerged female wasps were weighed to estimate the median weight of a species.

Analyses

Large datasets of the measured parameters (wasp body weight, prey body weight and number of stings delivered to a prey specimen) passed the normality tests only for the wasp species with the lowest numbers of observations. Only part of these datasets could be normalised using logarithm or square-root transformation. Therefore, we used simple non-parametric estimates where possible. For instance, the relative variability of prey size was estimated as a ratio between the inter-quartile (25%–75%) range of prey weight and the median weight of a female wasp.

The dependence of stinging effort against prey size was considered a linear regression, described by the function $s(w) = s_m + s_s w$. Here $s(w)$ is the total number of stings delivered to a prey specimen; w is the weight of a prey specimen; the intercept s_m (minimum of stings) reflects an estimated minimal stinging effort applied to a victim (the number of stings applied to a hypothetic prey of zero weight); s_s (size-dependent stings) is an estimated increment of stinging effort per prey weight unit; the product $s_s w$ is an estimated number of prey size-dependent stings delivered to a prey specimen of w weight. For the wasp species having a genetically fixed stinging pattern independent of the prey size ($s_s = 0$), the estimated total number of stings delivered to a prey would be equal to the estimated minimal stinging effort ($s(w) = s_m$). The share of the prey size-dependent stings on a prey of median weight was calculated as the ratio $s_s w_{med}/(s_m + s_s w_{med})$, where w_{med} is the median weight of prey for a particular wasp species.

The equation $s(w) = s_m + s_s w$ may be considered a simplified linear version of the handling time (or effort) function (Aljetlawi *et al*. 2004: eq. 4), irrespective of the predator's size and digestion time. For predatory wasps, such simplification is justifiable due to the low variability of the adult wasp body size in comparison with the wider size range of their larval prey, and due to the fact that their prey is stored in the nest rather than eaten. However, our equation includes an additional constant, the fixed minimal handling (stinging) effort s_m.

The significance of differences among the species-specific coefficients of the prey size-stinging effort regression was assessed and pairwise comparisons of these coefficients were fulfilled employing the General Linear Model (GLM) techniques (Homogeneity-of-slopes model, sigma-restricted parameterization, using StatSoft Statistica, release 7.0) and applying a Bonferroni correction to the significance level.

We used Pearson's correlation (r_P) as a measure of the adaptability of stinging effort to the prey size. We also used linear regression (r) to assess the effect of continuous predictors (relative size and relative variability of prey) on the species-specific r_P. We employed one-way ANOVA to ascertain the lack of effects of the categorical predictors, the wasp genus and prey type.

Results

Size of the predator and the prey

The studied wasp species represented a range of female median body weight from 12 mg (*S. debilitatus*) to 82 mg (*A. antilope*) (Table 1). They hunted prey with the median weights from 1–3 mg (*S. debilitatus*, *S. bifasciatus*) to

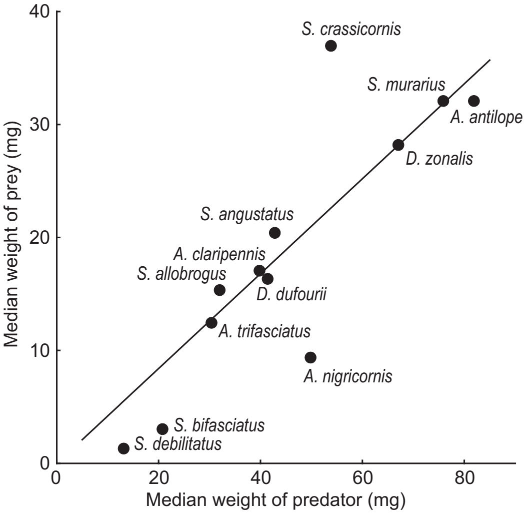

Fig. 1. Dependence of the median weight of prey on the median weight of female wasp in twelve Eumeninae wasp species.

31–37 mg (*A. antilope*, *S. crassicornis*, *S. murarius*). Grouped by genus, the species sets did not differ in the median weight of female (ANOVA: $F_{2,9} = 0.46$, $p = 0.65$) and the median weight of prey ($F_{2,9} = 0.10$, $p = 0.91$). Grouped by prey type (caterpillar *vs.* leaf beetle larva), the species sets did not differ in these parameters either (correspondingly, $F_{1,10} = 0.01$, $p = 0.93$ and $F_{1,10} = 0.49$, $p = 0.50$). Therefore, we presumed that the generic dependence and the prey type did not bias the observed effects of predator and prey size on the stinging pattern.

The size of prey correlated well with the size of predator (Fig. 1); the dependence could be described by a linear regression equation $y = (0.47 \pm 0.09)x$ (hereafter: mean value ± SE), where y was the median weight of prey and x was the median weight of female wasp; $r^2 = 0.73$, $p = 0.0003$. *S. debilitatus*, *S. bifasciatus*, *A. nigricornis* and *S. crassicornis* provided the largest residuals of the regression, hunting the relatively smallest (the first mentioned three species) and the relatively largest (the last mentioned species) prey. For the other eight studied species, the typical prey was of a similar relative size, ranging from 0.4 to 0.5 of the predator body weight (Table 1).

The relative variability of prey size (a ratio of inter-quartile range of weight to median weight of prey) ranged from 0.23 in *A. claripennis* and *S. debilitatus* to 0.72–0.81 in *A. trifasciatus*, *D. zonalis* and *S. allobrogus* (Table 1). At the available number of studied species, it did not significantly depend on the absolute size of predator (Fig. 2; regression fit $y = (0.34 \pm 0.14) + (0.004 \pm 0.003)x$; $r^2 = 0.17$, $p = 0.18$, only the intercept of the equation significant). The variability of prey size in relation to the size of predator (a ratio of the inter-quartile range of prey weight to the median weight of predator) did not depend on the size of predator either ($r^2 = 0.19$, $p = 0.15$).

Table 1. The median weight of female wasp and prey, the relative size of prey (ratio of the median weight of prey to the median weight of female wasp) and the variability of prey size (ratio of the inter-quartile range of weight to the median weight of prey) in twelve Eumeninae wasp species.

Wasp species	Median weight of female (mg)	*n* of weighed females	Median weight of prey (mg)	*n* of studied prey	Relative size of prey	Variability of prey size
A. antilope	82.0	109	32.0	513	0.39	0.69
A. claripennis	40.0	7	17.0	36	0.43	0.23
A. nigricornis	50.0	16	9.3	187	0.19	0.42
A. trifasciatus	30.5	154	12.4	330	0.41	0.78
D. dufourii	41.5	25	16.3	97	0.39	0.45
D. zonalis	67.2	32	28.1	44	0.42	0.81
S. allobrogus	32.0	1026	15.3	3041	0.48	0.72
S. angustatus	39.1	8	20.4	86	0.52	0.34
S. bifasciatus	18.6	117	3.0	496	0.16	0.43
S. crassicornis	47.4	36	36.9	270	0.78	0.64
S. debilitatus	12.2	14	1.3	70	0.11	0.23
S. murarius	64.6	75	31.3	556	0.48	0.51

Dependence of stinging effort on the prey size

Most of the studied wasp species applied on average from 3 to 17 stings per prey; an exception was *S. murarius* delivering an average of 48 stings to its prey (Table 2). There were no significant differences in the median number of stings delivered to a prey among the species of different genera (ANOVA: $F_{2,9} = 0.96$, $p = 0.42$) and between the species hunting caterpillars and those hunting leaf beetle larvae ($F_{1,10} = 2.87$, $p = 0.12$). Therefore, we assumed that neither generic dependence nor prey type essentially affected the dependence of stinging pattern on prey size.

A positive relationship between the weight of prey and the number of delivered stings, reflecting a species-specific adaptability of stinging behaviour, quantitatively estimated by the Pearson correlation (r_P), was significant ($p < 0.05$) in six studied species, close to significant ($0.05 < p < 0.1$) in three species, and not significant ($p > 0.1$) in the remaining three species. This dependence was stronger ($r_P \geq 0.2$) in *Discoelius* and most *Symmorphus* (except *S. bifasciatus* and *S. debilitatus*, both hunting relatively small and uniform prey), but weak in *Ancistrocerus* (Table 2).

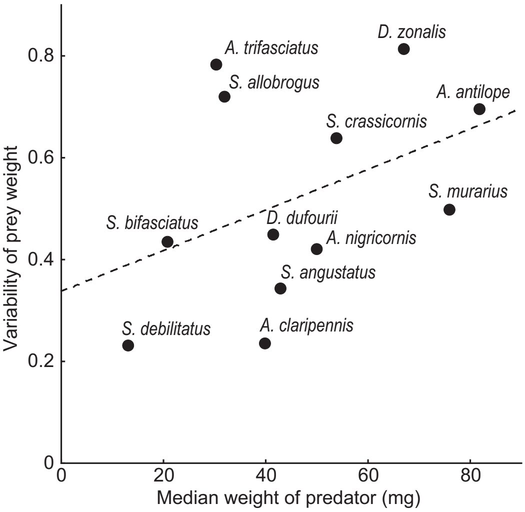

Fig. 2. Dependence of the relative variation range of the prey size (interquartile range of weight divided by the median weight of prey) on the absolute size of predator (the median weight of female wasp).

We tested the significance of differences amongst wasp species in their ability to adjust their stinging effort in relation to the prey weight using the GLM analysis. The differences in prey weight effect on the number of stings were significant only if eight ($F = 2.13$, $p = 0.037$) or less wasp species were included into the model, these representing more than 90 studied prey specimens (Table 1). A pairwise comparison of the dependence of stinging effort on the prey size confirmed that the adaptability of stinging effort of most studied wasps (with the only exception of *A. clar-*

Table 2. The number of stings per prey specimen (mean ± SE) and the parameters of the dependence of stinging effort on the prey size: Pearson's correlation (r_P), the estimated minimum stinging effort (s_m) and the estimated prey size-dependent increment of stinging effort (s_s). Number of the studied prey: *see* Table 1.

Wasp species	Stings per prey	r_P	s_m (stings)	s_s (stings/mg)
A. antilope	16.9 ± 1.1	0.08*	12.6 ± 2.6	0.13 ± 0.07*
A. claripennis	4.6 ± 0.4	ns	5.1 ± 1.9	ns
A. nigricornis	3.7 ± 0.3	ns	3.2 ± 0.7	ns
A. trifasciatus	7.4 ± 0.9	0.12	3.7 ± 2.0*	0.31 ± 0.14
D. dufourii	9.8 ± 0.4	0.24	7.3 ± 1.1	0.16 ± 0.06
D. zonalis	17.6 ± 1.4	0.35	11.3 ± 2.9	0.21 ± 0.09
S. allobrogus	8.9 ± 0.1	0.30	6.0 ± 0.2	0.19 ± 0.01
S. angustatus	11.0 ± 0.4	0.20*	8.0 ± 1.7	0.14 ± 0.08*
S. bifasciatus	8.6 ± 0.1	0.06*	8.2 ± 0.3	0.12 ± 0.09*
S. crassicornis	16.8 ± 0.7	0.41	7.5 ± 1.4	0.24 ± 0.03
S. debilitatus	3.1 ± 0.2	ns	2.4 ± 1.0	ns
S. murarius	48.0 ± 1.6	0.20	35.7 ± 3.1	0.32 ± 0.07

* = significant at $0.05 < p < 0.1$; ns = not significant ($p > 0.1$).

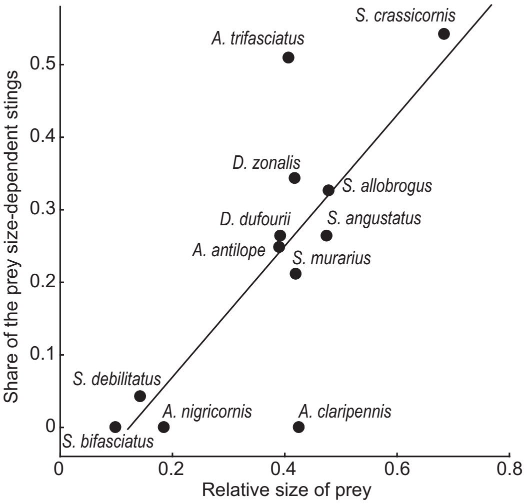

Fig. 3. Dependence of the prey size-dependent stinging effort (share of the prey size-dependent stings on a prey of median weight) on the relative size of prey (the median weight of prey divided by the median weight of female wasps).

ipennis) quantitatively differed from the adaptability of at least some other species (Table 3).

Employing a linear regression, we estimated the parameters of this dependence: the intercept that was considered a minimum needed number of stings (s_m) and the increment of stinging effort per prey weight unit (s_s) (Table 2). Multiplying the latter by the median weight of prey (w_{med}) of each wasp species, we calculated the estimated number of prey size-dependent stings on the prey of median size ($s_s w_{med}$).

The wasps hunting relatively larger prey applied a higher number of these additional, prey size-dependent stings to their victims: the share of these stings on a prey of median weight, $s_s w_{med}/(s_s w_{med} + s_m)$, significantly depended on the relative size of their prey (regression fit $y = (–0.11 \pm 0.09) + (0.90 \pm 0.23)x$, $r^2 = 0.60$, $p = 0.003$; the intercept is not significant) (Fig. 3).

Dependence of stinging effort on the variability of prey size

The wasp species hunting prey of a relatively more variable size applied a higher number of the size-dependent stings, additional to the basic stinging pattern: the estimated share of such

Table 3. Pairwise comparison of the species-specific linear regression between the weight of prey and the number of stings: absolute values of standardized regression coefficients (β) and their standard errors (GLM: homogeneity-of-slopes model, sigma-restricted parameterization). Number of the studied prey: *see* Table 1.

Wasp species	*S. murarius*	*S. debilitatus*	*S. crassicornis*	*S. bifasciatus*	*S. angustatus*	*S. allobrogus*	*D. zonalis*	*D. dufourii*	*A. trifasciatus*	*A. nigricornis*	*A. claripennis*
A. antilope	0.34 ± 0.06	ns	ns	ns	ns	0.21 ± 0.04	ns	ns	0.20 ± 0.08*	0.19 ± 0.09*	ns
A. claripennis	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
A. nigricornis	0.39 ± 0.07	ns	0.19 ± 0.08*	0.56 ± 0.08	0.43 ± 0.16*	0.13 ± 0.04	0.42 ± 0.10	0.40 ± 0.18*	ns		
A. trifasciatus	0.44 ± 0.06	ns	ns	0.21 ± 0.08*	ns	0.10 ± 0.04*	ns	ns			
D. dufourii	0.29 ± 0.10*	0.53 ± 0.20*	ns	ns	ns	ns	ns				
D. zonalis	0.18 ± 0.09*	0.48 ± 0.18*	ns	0.18 ± 0.08*	ns	0.12 ± 0.04					
S. allobrogus	0.53 ± 0.02	ns	ns	0.16 ± 0.04	ns						
S. angustatus	0.27 ± 0.13*	0.56 ± 0.20*	ns	ns							
S. bifasciatus	0.42 ± 0.05	0.56 ± 0.15	ns								
S. crassicornis	0.40 ± 0.07	ns									
S. debilitatus	ns										

* = difference not significant after Bonferroni correction ($0.00075 < p < 0.05$); ns = difference not significant ($p > 0.05$).

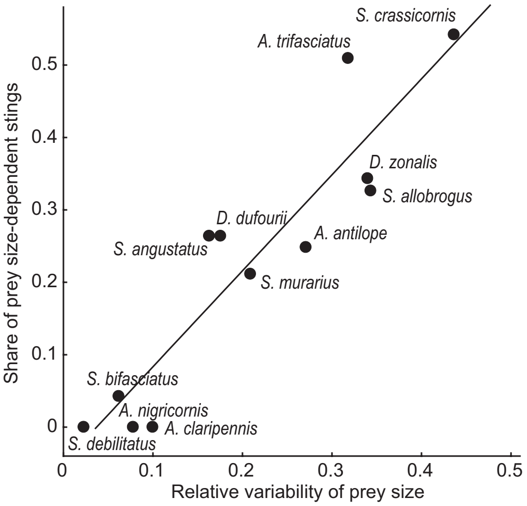

Fig. 4. Dependence of the prey size-dependent stinging effort (share of the prey size-dependent stings on a prey of median weight) on the relative variation of the prey size (the interquartile range of prey weight divided by the median weight of female wasps).

stings on a prey of median size was significantly larger in the species using a wider prey size range (Fig. 4; linear regression fit $y = (-0.05 \pm 0.04) + (1.33 \pm 0.18)x$, $r^2 = 0.84$, $p = 0.00002$; the intercept is not significant).

The ability of a female wasp to adapt its stinging effort more precisely to the size of prey also significantly positively depended on the size range of the prey exploited by the wasp species. This dependence could be described by a linear regression equation $y = (-0.02 \pm 0.05) + (0.88 \pm 0.19)x$ ($r^2 = 0.67$; $p = 0.001$; the intercept is not significant), where y is the adaptability (the species-specific r_P of a correlation between the weight of prey and the number of applied stings), and x is the relative variability of prey size (the ratio between the interquartile range of weight and the median weight of prey divided by the median weight of female wasp).

The effect of the relative size variability of the exploited prey on the adaptability of stinging effort varied among the studied wasp genera (Fig. 5). For the *Discoelius* and *Symmorphus* species, a wider prey size range resulted in nearly a two-fold increase in the ability to adjust the stinging effort [$y = (-0.01 \pm 0.03) + (0.92 \pm 0.10)x$, a continuous line in Fig. 5; $r^2 = 0.94$; $p = 0.00008$; the intercept is not significant] compared with the *Ancistrocerus* species [$y = (-0.04 \pm 0.01) + (0.48 \pm 0.04)x$, a dotted line in Fig. 5; $r^2 = 0.98$; $p = 0.008$].

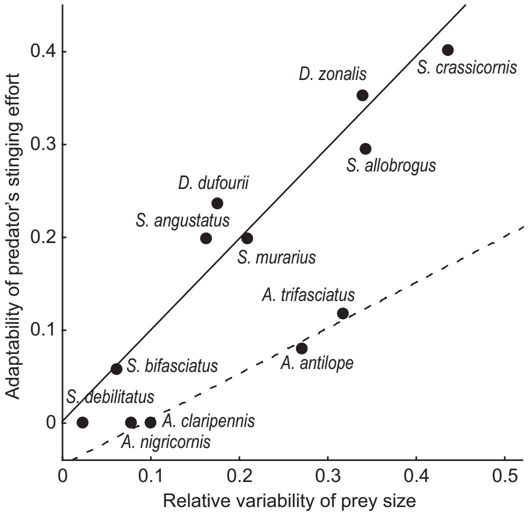

Fig. 5. Dependence of the predator's ability to adjust its stinging effort (r_P of a correlation between the weight of prey and the number of stings delivered to it) on the relative variation of the prey size (the interquartile range of prey weight divided by the median weight of female wasps). Continuous line: the regression fit for *Discoelius* and *Symmorphus* species; dotted line: the regression fit for *Ancistrocerus* species.

Discussion

The stinging pattern of predatory wasps includes a set of regular stings (C2SP, C4SP, etc.) aimed at the main 'locomotor' ganglia of their prey (Steiner 1986). It is usually supplemented by additional stings scattered throughout the body segments of the prey (Budriene & Budrys, 2005a). It was shown for several wasp species that the total number of delivered stings may positively depend on the size of prey (Budriene & Budrys 2005b). In this study, we demonstrated that the number of additional, prey size-dependent stings and the quantitative parameters of the dependence of stinging effort on the prey body size are species traits of prey handling behaviour in predatory taxa, which may significantly differ in closely related species or genera. Presumably, these traits may affect the evolutionary pathways of the predator's hunting behaviour and niche parameters, such as widening or shifting the exploited prey spectrum.

The possibility to use a wider size range of prey is considered an advantage for large predators and a constraint for small ones (Coelho & Hoagland 1995, Coelho & Ladage 1999, Grant 2006). In fact, the smallest studied wasps (*S. bifasciatus*, *S. debilitatus*) hunt prey of a more uniform size, whereas the size variability in prey of the largest wasps (*A. antilope*, *D. zonalis*) is considerably higher (Fig. 2). However, at least for the studied species set, the dependence between the relative variability of prey weight and the wasp weight was not significant. It means that compared with the small wasp species, the larger species do not benefit a lot from their size in hunting prey of a relatively wider size range.

A higher share of the flexible, prey size-dependent effort in the prey handling behaviour was typical of the species using a larger prey (Fig. 3). These results are congruent with the data on the behaviour of predatory crustaceans in the Baltic Sea (Aljetlawi *et al.* 2004) or coccinellid larvae feeding on mealybugs (Milonas *et al.* 2011). According to these studies, the handling time of small predators positively depends on the size of prey, while the handling time of large predators does not depend on it. In our case, the predatory wasps hunting the relatively largest prey (i.e. the smallest predators in relation to it) demonstrated the highest dependence of stinging effort on the size of prey. On the contrary, the stinging pattern of species exploiting relatively small prey (the largest predators in comparison with their prey) depended little on their size.

The relative variability of prey size affected the species-specific share of the additional, prey size-dependent stinging effort to an even greater degree than the relative size of prey ($r^2 = 0.84$ *vs*. $r^2 = 0.60$) (Fig. 4). This dependence demonstrates that predatory species exploiting a wider size range of prey are under selection pressure to evolve a more flexible handling behaviour, or otherwise, a more adaptable handling behaviour of a predator allows exploiting a wider range of prey.

The parameters of this adaptability of the handling behaviour were species-specific: the regression between the prey size and stinging intensity significantly differed among phylogenetically related species of one genus hunting prey of the same type, as in the studied cases of the *Symmorphus* species, exploiting larvae of Chrysomelinae, and some *Ancistrocerus* species, hunting caterpillars (Table 3).

A simpler and more standardised stinging pattern of most *Ancistrocerus* wasps usually includes 2–4 obligatory stings to prey's throat and metathorax (the C2SP) and is supplemented by additional scattered stings, particularly characteristic of stinging behaviour of *A. antilope*. In general, this stinging pattern seems to be less dependent on prey size than stinging of prey by *Discoelius* and most *Symmorphus* species. The assumption that the C2SP is suitable for paralysing the central nervous system of a caterpillar is supported by the fact that *S. debilitatus*, the only studied species of *Symmorphus* that hunts caterpillars, also paralyses its prey by just two stings (Table 2: s_m; *see* also Budriene & Budrys 2005a), one directed to throat or prothorax and the second to the first abdominal segment.

We presume, therefore, that the evolution of prey handling behaviour in predatory wasps, as well as other predators, could result in two different tactics of subduing their prey. One of them includes elaboration of precise techniques for optimal prey immobilisation, aimed at the most vulnerable structures of its body, e.g. the main centres of nervous or circulatory system. The efficiency of such techniques is less dependent on the relative prey size. However, their application implies an evolutionary stability of the used prey spectrum. The second type of tactics includes causing less precise and less efficient damage to the prey, though the amount of this damage depends on the size or resistance activity of the prey. Predators using the latter type of handling behaviour may have to apply a relatively higher effort to the prey of the same size than the users of the former tactics. However, they may benefit from attaining an ability to use a wider prey spectrum. In addition, they can save energy and apply a lesser effort to subdue small prey, thus keeping a constant rate of handling effort per prey size unit.

Among the studied predatory wasps, the caterpillar-hunting species *A. claripennis*, *A. nigricor-*

nis and *S. debilitatus* demonstrate the first type of hunting tactics. For all these wasps, the estimated fixed minimum of stinging effort (s_m) is approximately equal to the observed mean number of stings per prey, whereas the size-dependent increment of stinging effort (s_s) has low and statistically insignificant values (Table 2). *Symmorphus bifasciatus*, hunting relatively small leaf beetle larvae, is close to this group as well (Fig. 4). For these wasps, the handling effort function $s(w) = s_m + s_s w$ becomes a constant $s(w) = s_m$.

The remaining studied wasp species seem to apply the second type of handling tactics. They immobilise their prey by less precise but more numerous stings, the number of which depends on the size and possibly the resistance activity of the prey. The estimated number of prey size-dependent stings comprises more than 20% of all stinging effort applied to a prey of an average size in this group of species; this behavioural parameter reaches 50% in *A. trifasciatus* and 55% in *S. crassicornis* (Fig. 3).

Comparison of the dependence of stinging effort on prey size demonstrates that the evolutionary potential of behavioural adaptability, allowing some wasps to exploit relatively larger prey (Fig. 3) or a wider size spectrum of prey (Fig. 4), is higher among *Discoelius* and *Symmorphus* species than among *Ancistrocerus* species. All representatives of *Ancistrocerus*, the wasps demonstrating a relatively more uniform C2SP stinging pattern, use only caterpillars as their prey. In contrast, *Discoelius* species provision their brood cells with a variety of caterpillars and larvae of sawflies; some *Symmorphus* species hunt caterpillars, while others use larvae of Chrysomelidae or Curculionidae beetles. We assume that a higher adaptability potential of prey handling behaviour has allowed an evolutionary widening of the intra-specific spectrum of prey, as in *Discoelius* wasps, or an easier evolutionary switching from one prey type to another, as among *Symmorphus* species.

This study is just one step towards the understanding of the behavioural adaptability of prey handling in predatory wasps. The physiological parameters of prey handling, like the amount of venom per sting and the immobilising efficiency of the venom, may be important as well. We cannot exclude the possibility that the wasp species demonstrating a more constant stinging pattern may be able to differentiate the amount of venom delivered in accordance to the size of prey, instead of changing the number of stings. For the wasps with a flexible stinging pattern, part of their stinging variation may be caused by a variable susceptibility of prey species to the venom. These aspects of stinging behaviour have to be further clarified.

Behavioural characteristics of predators are considered essential for dominating feeding strategies and predator size–prey size distributions in ecosystems and their food webs (Loeuille 2010, Carey & Wahlab 2011). We presume that two marginal types of prey handling tactics, the fixed and the flexible, or intermediate prey handling styles are a part of the hunting behaviour of all insect and non-insect predators. The example of the eumenine wasps demonstrates that the quantitative characteristics of the adaptability of the subduing of prey may be considered species traits related to their trophic specialisation and to the size range of the exploited prey. These behavioural traits also reflect the evolutionary potential of a predatory species to widen or shift its prey spectrum.

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