

Use of conditional prey attack strategies in two generalist ground spider species

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Abstract

Generalist predators have evolved a variety of behavioural adaptations in prey capture to effectively subdue different prey types. Such predators use a conditional hunting strategy. Among spiders, representatives of Gnaphosidae are known to use either venom attack (subduing prey with venom) or silk attack (subduing prey with silk). In this study, we aimed to test the hypothesis of the conditional use of prey capture strategy (venom *versus* silk attack) in two species, *Drassodes* sp. and *Zelotes* sp. We also measured the size of their venom glands and the number of their piriform glands in order to reveal whether behavioural adaptations are paralleled with morphological ones. As prey, we used other spiders of variable sizes as these are considered dangerous prey. We found that *Drassodes* used mainly silk attack, while the majority of *Zelotes* used venom attack. The probability of using silk attack increased with predator/prey body length ratio in *Drassodes*, but not in *Zelotes*. Then, we disabled silk use in individuals of both species. All disabled *Drassodes* used venom attack, but about half of individuals attempted to use silk attack first. All *Zelotes* used venom attack, and none attempted to use silk attack first. We found significantly larger venom glands in *Drassodes* than in *Zelotes*, while the number of piriform silk glands was similar. The behavioural adaptations are, thus, not paralleled with morphological (i.e., venom and silk gland size) ones. Our results suggest that both *Drassodes* and *Zelotes* can use both attack strategies with similar efficacy.

KEYWORDS

Araneae, *Drassodes*, silk immobilization, venom gland, *Zelotes*

1 | INTRODUCTION

The behavioural repertoire used in prey searching and prey capture is often very complex both in generalist vertebrate (e.g., fish, van Wassenberg et al., 2006; frogs, Valdez & Nishikawa, 1997; lizards, Lappin & German, 2005) and invertebrate predators (beetle, Murdoch & Marks, 1973; spiders, Jackson, 1992; Tsai & Pekár, 2019). The fact that generalist predators can often shift between active (kinematic) and ambush (si- and-wait) foraging strategies Zoroa et al., 2011; Ross & Winterhalder, 2015) suggest that such behaviour is also plastic. These predators have evolved such a repertoire because they deal with a

variety of prey types. To catch a prey, they are expected to select the most successful capture strategy for a particular prey type from available alternative strategies (Monroy & Nishikawa, 2011). For example, the active strategy that maximizes success in capturing small, highly mobile prey might be much less successful for capturing larger, slowly moving prey, or prey that is capable of defending itself from predation (e.g., Lappin & German, 2005; Sherbrooke & Schwenk, 2008). Thus, the decision of which type of strategy to use is conditioned/optimized also by many other factors, such as prey defensive characteristic, prey size, prey density, and the predator's physiological state (van Wassenberg et al., 2006; Willemart & Lacava, 2017).

Spiders are considered the most diverse group of terrestrial predators, with foraging behaviour that is largely opportunistic (Pekár et al., 2012, 2017). Most spider predators are euryphagous and generalists, and their diets consist mainly of insects and other arthropods, including other spiders and/or conspecifics (e.g., Heuts & Brunt, 2001; Guseinov, 2006). Spiders are expected to use a variety of foraging strategies (Pekár & Toft, 2015), which should result from complex interactions between the prey and predator (Brodie & Brodie, 1999). Similarly, as in other generalists, the use of these prey-capture strategies is often conditional upon the type of prey and its defensive characteristics, particularly dangerousness and size (Mukherjee & Heithaus, 2013; Tsai & Pekár, 2019). When faced with several different preys, the spider predator may use different optimal capture behaviours for each depending not only on the type of prey but also on the prey-specific balance of costs (Bolnick & Ferry-Graham, 2002; van Wassenberg et al., 2006). Therefore, generalist spiders are an excellent model for studying possible conditional foraging behaviour in prey–predator systems.

Foraging strategy comprises a series of behaviours effective at different stages of the prey capture sequence, beginning with approach and ending with attack or immobilization. Conditional foraging strategies have been reported in a range of spider representatives. For instance, *Yllenus arenarius* Menge (Bartos & Szczepko, 2012) used prey-specific capture strategies towards prey, exhibiting both high and low escape risk. Another intriguing example is the spitting spider, *Scytodes pallida* Doleschall, which regulated the amount of spit depending on the size of prey and its struggling intensity (Clements & Li, 2005). *Portia* spiders have capacities (Wilcox & Jackson, 1998) to use alternative capture strategies, with or without the use of a web (Jackson & Hallas, 1986). Such switching foraging behaviour remains little known in other generalist spider predators.

Similarly, spiders of the family Gnaphosidae use two different capture strategies to immobilize prey: silk or venom attack (Wolff et al., 2017). Silk attack is a non-contact form of prey immobilization, while venom attack (and venom injection) requires direct contact between the predator and prey. In general, silk attack has been broadly accepted to be more efficient (Pekár & Toft, 2015) and presumably a safer strategy than venom attack (Gilbert & Rayor, 1985; Schmidt, 1990), especially when the prey is dangerous. However, gnaphosid spiders are known to often hunt dangerous prey, such as ants or spiders (Jarman & Jackson, 1986; Michálek et al., 2018), beside other types of prey (Michálek et al., 2017, 2018; Petráková Dušátková et al., 2020), which increases the frequency of silk attacks by these spiders.

Frequent silk use in such generalist species has led to the modification of the spinning apparatus, that is, anterior lateral spinnerets (ALS) produce sticky silk from the piriform gland (PI) during prey capture. Our recent comparative analysis of a number of gnaphosid genera showed that most genera used silk attack to immobilize particularly large prey, while a few genera used venom attack (Beydizada et al., 2020). Ancestral state reconstruction revealed that the use of silk for prey immobilization was as probable as venom attack for ancestors (Beydizada et al., 2020). It seems that the production of both silk and venom is costly, so there should be a trade-off in using them,

albeit in differing proportions. Thus, most species using venom attack, for example, should have larger venom glands than species that use mainly silk attack. The size of venom glands correlates with body size and bigger venom glands are characteristic of generalist spiders (Pekár et al., 2018).

Our aim here was to investigate how fixed the use of a capture strategy is in generalist ground spider predators of the family Gnaphosidae. We selected two genera, *Drassodes* and *Zelotes*, known to use different attack strategies with different frequencies (Beydizada et al., 2020). We performed a manipulative experiment in which the use of one strategy was disabled. In addition, we also performed measurements of the venom (size) and silk (number of piriform) glands in order to reveal whether behavioural adaptations are paralleled with morphological ones. We predicted that the venom glands would be larger in species that use them for immobilization and *vice versa*.

2 | MATERIAL AND METHODS

2.1 | Study species

Specimens of *Drassodes* sp. ($N = 50$: 48 juveniles and two subadult females) and *Zelotes* sp. ($N = 20$: 6 juveniles, three subadult females, three subadult males, and eight adult females) were collected by hand either under stones or under the bark in the territory of Czechia (Hády, Brno, August–October, 2020). *Zelotes* sp. represented a mixture of *Zelotes*, *Drassyllus*, and *Trachyzelotes* individuals according to the World Spider Catalog (2021). Collected specimens were placed singly in Eppendorf tubes (2.5 ml) with punctured lids, placed with a piece of wet paper tissue in a plastic bag, and transported to the laboratory. To standardize their satiation level, spiders were fed with other spiders (see below). If a spider did not capture prey, it was considered unmotivated to eat (i.e., satiated or preparing to moult), and those individuals were again offered prey the next day. After feeding, spiders were kept in a chamber at low temperature (10°C) and under a short-day regime (LD = 8:16) prior to their use in experiments in order to slow their ontogenetic development.

As prey, we used spiders (juvenile and subadult stages) of *Pardosa* sp. ($N = 50$), *Mangora acalypha* ($N = 18$), and *Xysticus* sp. ($N = 2$). They were collected by hand around the university campus (Czechia: Brno). Prey spiders were kept singly in plastic containers/tubes (1.5 ml) with a piece of moist paper tissue. All prey animals were held under the following conditions: 4°C, LD = 8:16.

All spiders used were identified using the key by Nentwig et al. (2021). After identification, the prosoma length of all individuals was measured to the nearest 0.1 mm using an ocular ruler within an Olympus stereomicroscope.

2.2 | Experimental procedure

One week before using *Drassodes* (mean prosoma length \pm SEM = 2.67 ± 0.004 mm) and *Zelotes* (mean prosoma

length \pm SEM = 2.22 ± 0.05 mm) in experiments, all spiders were moved to room temperature ($23 \pm 1^\circ\text{C}$). During this period, these spiders were not fed. Then, *Drassodes* or *Zelotes* individuals were placed singly in Petri dishes (diameter 3.5 cm or 5.5 cm; height 1.5 cm, depending on their body), and the experimental trial began after at least 1 h of acclimatization. Each individual was offered one specimen of the prey so that the body size of the prey was smaller than the body size of the predator. *Pardosa* spiders (mean prosoma length \pm SEM = 2.19 ± 0.002 mm) were used as prey for *Drassodes*. As *Pardosa* spiders were too large compared to *Zelotes*, we used *Mangora* (mean prosoma length \pm SEM = 1.26 ± 0.01 mm) and *Xysticus* spiders (mean prosoma length \pm SEM = 0.95 ± 0.10 mm) instead because these were smaller than *Zelotes* and easily available. Predator–prey interactions were recorded for up to approximately 60 mins using a video camera (Canon Legria HF R606). Each video recording began when the prey was released into the dish. The trial ended when the predator spider had killed and consumed the prey or when one hour had elapsed.

Then, after six days, the *Drassodes* individuals were split randomly into two equal groups, 'sealed' and 'control', each containing 25 individuals. Each individual was anesthetized by means of CO_2 for a period of 1–2 minutes and then placed into a dish under a stereomicroscope. Melted beeswax was applied to the tips of all spinnerets (the sealed group) or to the ventral side of the abdomen close to the spinnerets (the control group) by means of fine soldering iron. The spiders from the sealed group, thus, could not produce silk.

In *Zelotes* spiders, as the number of individuals was smaller, all individuals were manipulated. After six days, all *Zelotes* individuals were anesthetized (as above), and the tips of their spinnerets were damaged by pressing them with a fine hard pincer. We could not use beeswax in *Zelotes* as their spinnerets were too small.

One day after treatment, the spiders were used in prey-capture trials. *Drassodes* and *Zelotes* spiders were each offered prey that were approximately 50% smaller in size (i.e., the prey's body length was similar to the predator's prosoma length, Figure S1). All trials were conducted in similar environmental (room) conditions as mentioned above. *Drassodes* or *Zelotes* spiders were released singly into Petri dishes (as above) and left approximately for 1 h to acclimatize. Then, the prey was released, and the interactions were recorded using a video camera. Each trial ended when the predator captured the prey or when one hour had elapsed.

The movies with hunting sequences were analysed (Video S1). We recorded the capture behaviour used, the hunting success, and the latency to attack (the period between the first contact with the prey and the prey attack, either by silk or venom).

2.3 | Venom and silk glands

We measured the size of venom glands and counted the number of silk glands in juvenile *Drassodes* ($N = 7$) and *Zelotes* ($N = 7$) individuals. Spiders were kept in Eppendorf tubes and starved for about 3 days prior to dissection of the glands. To dissect venom glands, the

spiders were first anaesthetized with CO_2 and then mounted upside-down on a paraffin stub by means of a thin pin (pushed through the posterior part of the prosoma). Then, using fine pincers, the base of the chelicerae was removed, which released the glands from the prosoma. Using fine pincers, the dissected glands were placed into a drop of physiological solution (NaCl 0.9%) on a glass slide. Similarly, the anterior lateral spinnerets along with their associated silk glands were dissected from four individuals of both *Drassodes* and *Zelotes*. The number of piriform glands was counted. The dimensions of the venom glands—the widths ($2r$) and lengths (d)—were measured using an ocular ruler in an Olympus SX stereomicroscope. The volume of the gland (V) was estimated by assuming a cylindrical shape ($V = d\pi r^2$). The length of the prosoma was also measured for each individual.

2.4 | Statistical analyses

Paired t test with Welch approximation was used to compare latencies to attack because the variance between the two experimental groups differed. Mc Nemar's test was used to compare the proportions of the use of venom attack between experimental groups. Generalized linear models with binomial error structure (GLM-b) were used to test the relationship between the prey-to-predator body size ratio (the ratio of the prosoma length of the prey to the prosoma length of the spider) and the attack probability separately for *Drassodes* and *Zelotes* (Pekár & Brabec, 2016). The relative volume of the venom glands and the relative number of silk glands (i.e., normalized to prosoma length) were compared between species using GLMM implemented within generalized additive models from the mgcv package (Wood, 2006). For the venom gland volume, a gamma error structure was used, while for the number of piriform glands, Poisson's error structure was used. GLMM was used because there were two measurements per individual. All statistical analyses were performed within the R environment (R Core Team, 2017).

3 | RESULTS

3.1 | Venom and silk glands

The relative volume of venom glands was significantly larger in *Drassodes* than in *Zelotes* (GLMM-g, $F_{1,12} = 14.0$, $p = .001$, Figure 1). The number of piriform glands was not significantly different between *Drassodes* and *Zelotes* after correcting for their prosoma length (GLMM-p, $\chi^2_1 < 0.1$, $p = .84$).

3.2 | Prey capture behaviour

Unmanipulated *Drassodes* and *Zelotes* spiders used one of three attack strategies: silk attack followed by biting, that is, the quick immobilization of prey by silk from a short distance and then biting

prey (observed in both species); venom attack, that is, the prey was grasped with the forelegs, pulled towards chelicera, and immobilized using a bite and venom injection (in both species); and venom attack followed by silk application, that is, the prey was grasped and bitten and then silk was applied on the legs of prey while the prey was held in the predator's chelicerae (in *Drassodes* only). These two strategies were combined into one, henceforth referred to as 'venom attack'.

All unmanipulated *Drassodes* individuals captured and consumed *Pardosa* prey ($N = 50$). A great majority of individuals used silk attack

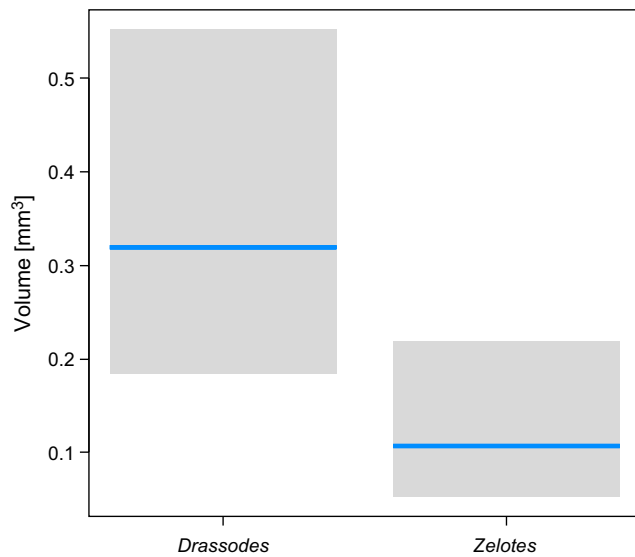


FIGURE 1 Comparison of venom gland volume between *Drassodes* and *Zelotes*. Blue lines represent the mean, grey boxes represent 95% confidence intervals of the mean

(Figure 2a). There was a positive relationship between the ratio of predator/prey length and the use of silk attack (GLM-b, $X^2_1 = 7.4$, $p = .007$, Figure 3), that is, as prey size increased compared to *Drassodes* size, silk attack was more frequently used.

Similarly, all *Drassodes* individuals with sealed spinnerets captured prey ($N = 25$), and all used venom attack (Figure 2a). However, 40% of individuals tried to use silk attack first. All these individuals also used silk attack before manipulation. There was no significant difference in the latency to attack between the unmanipulated and sealed groups (Paired t-test, $t_{24} = -1.5$, $p = .146$); the attack occurred on average after 304.1 s ($SE = 25.0$).

Also, 92% ($N = 25$) of *Drassodes* individuals from the control group captured prey. However, a great majority ($N = 21$) of individuals used venom attack (Figure 2a). There was a significant difference in the frequency of venom attack between the unmanipulated and control groups (McNemar's test, $X^2_1 = 8.1$, $p = .0044$), revealing the effect of experimental manipulation. There was a marginally significant difference in the latency to attack between unmanipulated and control groups (Paired t-test, $t_{22} = 2.0$, $p = .055$): the attack occurred on average after 203.0 s ($SE = 20.1$). Compared to their capture behaviour before manipulation, 43% of individuals ($N = 23$) shifted from the silk to venom attack, while the remaining individuals used the same attack behaviour. Only two individuals used venom attack in both trials.

All unmanipulated *Zelotes* spiders captured prey ($N = 20$). The majority of individuals used venom attack (Figure 2b). There was no significant relationship between predator/prey size ratio and the use of venom attack (GLM-b, $X^2_1 < 0.1$, $p = .79$).

Similarly, all *Zelotes* individuals with damaged spinnerets captured prey ($N = 20$), and all individuals used venom attack (Figure 2b).

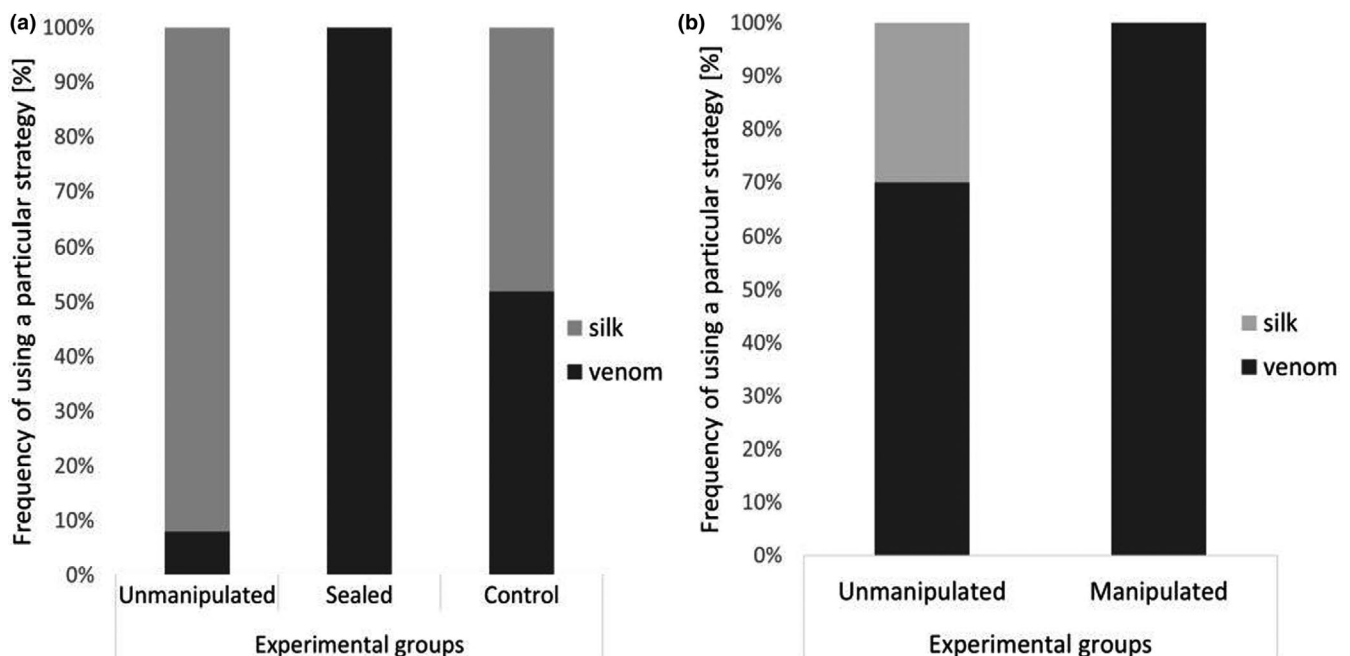


FIGURE 2 Comparison of relative frequencies of the use of two attack strategies (silk or venom attack) in (a) three experimental groups of *Drassodes* and (b) two experimental groups of *Zelotes* individuals

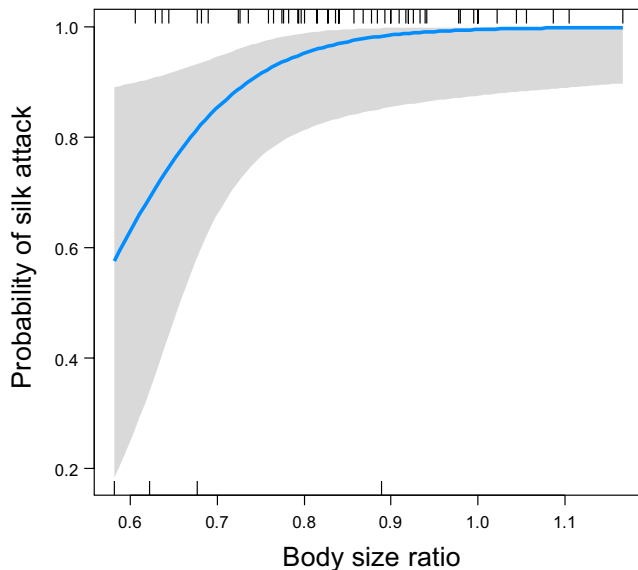


FIGURE 3 Relationship between the probability of using venom attack for the immobilization of prey and the prey-to-predator prosoma length ratio in *Drassodes*. The estimated logit model is shown with a 95% confidence band (grey area). Rugs along horizontal axes show binary measurements (0, 1)

No individual tried to use silk attack. However, 30% of individuals shifted from silk (before manipulation) to venom attack, so there was a significant difference between the groups in the use of venom attack (McNemar's test, $X^2_1 = 4.1$, $p = .04$). There was no significant difference in the latency to attack between unmanipulated and manipulated groups (Paired t-test, $t_{37} = -1.3$, $p = .16$): the attack occurred on average after 1055 s ($SE = 46.9$).

4 | DISCUSSION

We found that the capture strategies are not fixed but exchangeable in both *Drassodes* and *Zelotes*. If the strategies provide similar benefits and exert similar costs, then we expect them to be used with similar frequency. The results also show that the results of treatment (the inability to use silk attack) did not affect the success of prey-capture, though we did not measure the costs of each strategy. However, some spiders did not use the available strategy directly but tried to immobilize the prey by silk. This indicates that silk attack is a preferred strategy to venom attack probably because it is less costly.

The use of silk attack increased considerably with the relative size of the prey in *Drassodes*, but not in *Zelotes*. A similar relationship was observed in other spiders. For instance, in the orb-web spider of the genus *Argiope*, prey size determined the structure, properties, and amount of the silk material used (Murakami, 1983). We assume that the attack strategy is more plastic and exchangeable in *Drassodes* than in *Zelotes*. For *Zelotes*, the size of prey may not be as important as the type of prey which we, however, did not study here.

It is also interesting to note that the attack strategy of *Drassodes* was similar to other gnaphosid generalist spiders, such as *Pterotricha*, *Scotophaeus*, and *Gnaphosa*, while the attack strategy of *Zelotes* was very similar to the attack behaviour observed in *Haplodrassus* and *Trychothyse* (see Beydizada et al., 2020). *Pterotricha*, *Scotophaeus*, and *Gnaphosa* switched to the silk attack with increasing prey size as done by *Drassodes*, whereas *Haplodrassus* and *Trychothyse* did not, which is similar to the behaviour of *Zelotes*. This indicates a certain degree of phylogenetic relatedness. However, this prey capture similarity among genera is not supported by the most recent phylogenetic analysis of Gnaphosidae. This analysis may not reflect true phylogenetic relationship as it was based only on morphological characters (Azevedo et al., 2018), or if it does, then the capture strategy is highly labile within Gnaphosidae.

There was a remarkable behavioural difference in how *Drassodes* and *Zelotes* responded to the new condition following treatment. Manipulated *Drassodes* tried to use silk to immobilize the prey, but not manipulated *Zelotes* individuals. We believe that there is some degree of preference in using either silk or venom among generalist gnaphosid spiders, although highly modified spinning apparatus characterizes the whole family Gnaphosidae. We cannot also exclude the possibility that the difference in the described behaviour could be because of the different treatment of the spinnerets and perhaps because of different preys used that possess different locomotory behaviour. *Pardosa* is an active hunting spider, while *Mangora* is a web-builder, and *Xysticus* is a sit-and-wait predator.

Recent behavioural as well as morphological investigations of gnaphosids have shown the anterior lateral spinnerets (ALS) to play an important role in prey capture, enabling ground spiders to subdue dangerous prey (Wolff et al., 2017). Indeed, the use of silk is associated not only with the size of the ALS (which produce sticky silk from piriform glands) but also with the number of spigots located on the ALS (Beydizada et al., 2020). Perhaps blocking the function of only the ALS would be ideal for investigating more exactly the role of these glands. However, due to the very small size of the studied specimens, it was too difficult to apply melted beeswax only on certain spinnerets while leaving other spinnerets untouched. Therefore, we had to block or damage all spinnerets.

Since the use of both biomaterials, venom and silk, is metabolically costly, there might be a trade-off in using them. In *Drassodes*, the prey is more often immobilized with silk. Thus, we expected that if less venom is used for prey immobilization, then it is because their venom glands are smaller. We failed to find support for this prediction. However, it might not be the venom gland volume but venom composition that matters. In prey-specialists, venom is more potent on particular types of prey (Michálek et al., 2019; Pekár et al., 2018). Interestingly, previous studies have reported that spiders should modulate venom release to avoid the considerable biochemical expense of regenerating depleted reserves (Malli et al., 1998).

In a recent article (Michálek et al., 2019), adaptations of strictly specialized and less specialized gnaphosid species were compared. The behavioural approach as well as venom/silk glands size and venom composition significantly differed between study species.

Smaller venom glands but larger piriform glands were found in less-specialized gnaphosid species (Michálek et al., 2019). The larger venom glands in *Drassodes* might be linked to its being a generalist species (Pekár et al., 2018), while the smaller venom glands in *Zelotes* indicate a more specialized habit. So, it seems that the trade-off between venom and silk materials is determined by the trophic strategy rather than by the specimen's body size.

The comparative morphological analysis of ALS (PI and MA glands) among some generalist ground spider representatives (Wolff et al., 2017) points to another key element, the sticky silk, in the evolution of araneophagy in ground spiders. The use of sticky silk for prey immobilization is well-known from other araneophagous web-building spiders, namely, cobweb spiders (Theridiidae) (Foelix, 1982). However, these have evolved an additional set of glands, the aggregate glands, which produce viscid glue, and their ALS are not modified (Coddington, 1989; Sahni et al., 2011). In gnaphosid spiders, the piriform glands (PI) have diversified (Wolff et al., 2017), which enables spiders to use sticky silk for effective prey immobilization. A similar adaptation has also been observed in pholcid spiders. Their piriform glands are enlarged (Huber, 2000), and this modification may also be related to a special wrapping attack (Huber & Fleckenstein, 2008; Jackson & Brassington, 1987). Despite the modification of their ALS spinnerets, pholcids retain the ability to spin attachment discs, but with modified shape. The modification of ALS seems to be a universal adaptation in all ground spiders, no matter whether they use venom or silk attack. This is supported by the absence of a significant difference in the number of PI between *Drassodes* and *Zelotes*.

In this article, we show the ability to shift attack behaviour in two generalist ground spiders. Their behavioural adaptations are highly plastic, enabling them to switch between strategies depending on the type of prey. Behavioural observations also showed the capture behaviour of *Zelotes* to be more stereotyped than that of *Drassodes*; thus, we believe there is a degree of trophic adaptation (preference in the use of attack strategies) in these spiders. However, the linking of certain morphological characters (larger venom glands in *Drassodes* and a smaller number of PI in *Zelotes*) to behavioural adaptations was not supported. Thus, our results suggest that behavioural adaptations are not paralleled with morphological ones.

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AUTHOR CONTRIBUTIONS

SP and NB conceived the study, designed the experiment, analysed the data, and wrote the manuscript. MR performed the morphological analysis and contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in [Depository of Terrestrial Invertebrate Research Group] at [https://www.sci.muni.cz/zoolecol/inverteb/?page_id=18].

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