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How oniscophagous spiders overcome woodlouse armour

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Abstract

Woodlice (Isopoda: Oniscoidea) are well defended by a heavy armour and many species have noxious secretions. Oniscophagy (feeding on woodlice) may be an important part of the biology of at least some members of the spider genus *Dysdera* (Dysderidae). Yet there little is known about the diet and possible specializations for feeding on woodlice in these spiders. *Dysdera* has unusual variability in mouthpart morphology, which may be related to the diet. Here, we investigate five species of *Dysdera* and consider the relationship between mouthpart morphology, capture frequency and prey-capture behaviour. We show that species with unmodified chelicerae readily capture a variety of arthropods, but refuse woodlice as prey, whereas species with modified chelicerae feed on woodlice and reject most of the other prey. Among the oniscophagic species, the grasping methods used during the capture of woodlice varied. Species with elongate chelicerae inserted one chelicera into the soft ventral side of the woodlouse and placed the other chelicera on the dorsal side of the woodlouse. Species with dorsally concave chelicerae quickly tucked their chelicerae under the woodlouse and bit the ventral side of the woodlouse's body. Species with flattened chelicerae inserted their chelicerae between the sclerites into the armour of the woodlouse.

Introduction

The fact that diet specialization might be a driving force behind morphological and behavioural diversification has been a frequent subject in the zoological literature ever since Darwin (1859) documented the relationship between beak morphology and diet for finches in the Galapagos Archipelago. Diet specialists often evolve remarkable morphological and behavioural adaptations, which are absent in diet generalists. With predators, in particular, our interest is in how these adaptations might increase the efficiency of capturing a principal prey and, at the same time, constrain the ability to capture an alternative prey (Ferry-Graham, Bolnick & Wainwright, 2002). Diet specialization may be severely disadvantageous when the principal prey becomes rare, and for this reason we expect to find diet specialization especially when the principal prey is common.

The literature on specialized predatory arthropods is biased towards aphid specialists (e.g. Hodek & Honěk, 1996) and ant specialists (e.g. Hölldobler & Wilson, 1990); woodlouse specialists are poorly studied. Yet specialization on woodlice might be common, as these detritus-feeding terrestrial crustaceans are dominant components of the ground-dwelling fauna in many habitats. Having a clumsy, slow-moving style of locomotion, woodlice may appear to be easy prey, but they have morphological, chemical and behavioural defences that appear to be insurmountable for many predatory arthropods (Gorvett, 1956). Glandular secretions make them evil smelling or indigestible for many predators (Sutton, 1980), and their heavily incrusted armour physically shields most of the woodlouse's body against the mouthparts of many potential predators. A woodlouse can protect the soft underside of its body behaviourally either by rolling up into a ball (rollers) or by clinging strongly to the substrate (clingers) (Schmalfuss, 1984). There are nevertheless a few arthropod groups, including scorpions (e.g. Kheirallah, 1979), harvestmen (e.g. Sunderland & Sutton, 1980), centipedes (e.g. Sutton, 1970), earwigs and ants (e.g. Sunderland & Sutton, 1980), true bugs (e.g. Kott, 2000), crickets (e.g. Paris & Sikora, 1967) and a few beetles (e.g. Dennison & Hodkinson, 1983; Whitehead, 1986), that include at least a few species that are reported to prey on woodlice occasionally. There are also reports of spider species from a variety of families that sometimes feed on woodlice (e.g. Pötzsch, 1966; Barmeyer, 1975; Sunderland & Sutton, 1980; Nentwig, 1986; Raupach, 2005).

Ants of the genus *Leptogenys* from tropical Africa and America are the only fully documented examples of predators that have become specialists that feed exclusively on woodlice. The morphological and behavioural adaptations by which these ants overcome the woodlouse's defences include elongated, thin and curved mandibles by which they grasp the rollers (Dejean, 1997): if the woodlouse fits between the mandibles they grasp it by its whole body, and if it is larger they grasp it by the edge of the shell (Dejean & Evraerts, 1997).

The spider genus *Dysdera* (Dysderidae) comprises 250 described species, almost all of which are restricted to small areas in the western Palaearctic, mainly around the Mediterranean basin (Platnick, 2006). Reports from the literature have long suggested that this genus contains species that specialize on woodlice (Bristowe, 1958). These spiders are non-web-building predators that search for prey on the ground at night. During the daytime, they stay hidden in silk retreats under stones or wood. The species in this genus also have varied, distinctive mouthparts that are used as characters in infrageneric taxonomy (Deeleman-Reinhold & Deeleman, 1988; Arnedo, Oromí & Ribera, 2001), but the functional significance of cheliceral morphology has not been investigated before.

Spider chelicerae are composed of two segments: a robust basal segment and a thorn-like fang with a poison gland orifice near its tip. In the majority of spiders, the chelicerae work synchronously against each other. Spiders use their chelicerae primarily for prey handling, but spider chelicerae may also function in burrow construction, courtship and defence (Bristowe, 1958). In the vast majority of spider species, there is remarkable uniformity in cheliceral morphology. This could be because spiders are usually non-selective predators and their mouthparts must have a structure sufficiently generalized to allow the capture of a wide range of prey. The best-known examples of specialized cheliceral morphology appear to be modifications with sexual dimorphism brought about by sexual selection (tetragnathids: Wiehle, 1963; theridiids: Bosmans & van Keer, 1999; salticids: Prószynski, 2004), apparently leading to male–female differences in feeding mechanics (Pollard, 1994).

Examples of cheliceral morphology having evolved specifically in the context of prey specialization are scarce. The best-documented example comes from Olive (1980), who showed a relationship between fang size, leg length and web mesh size and placement, and suggested that combinations of these traits allowed orb-web spiders to specialize on larger or smaller flying insects and on insects differing in their defence abilities. However, in general, spiders with special diets appear to have evolved behavioural and venom specialization rather than specialized cheliceral adaptations.

In *Dysdera*, cheliceral morphology tends to be the same in the juveniles, adult males and adult females of each species, and thus sexual selection is unlikely to be a driving force behind the evolution of variation in cheliceral morphology. Here, the hypothesis we consider is that the cheliceral variation seen in *Dysdera* is a product of dietary adaptation, with woodlice being the prey of particular importance. To date, there is published information on prey and predatory behaviour for two *Dysdera* species, *Dysdera erythrina* and *Dysdera crocata*, both of which have elongated chelicerae and are known to feed regularly on woodlice (Bristowe, 1958; Sunderland & Sutton, 1980; Hopkin & Martin, 1985; Raupach, 2005; Latreille, 1804). Analysis of prey remains found in their silk retreats and prey-capture experiments suggest that these species do not prefer any particular woodlouse species (Cooke, 1965*a*; Pollard *et al*., 1995). As the capture techniques of these spiders are similar, cheliceral elongation has been considered to be an adaptation allowing for efficient grasping of woodlice (Bristowe, 1958; Pollard, 1986). However, even if elongated chelicerae allow *Dysdera* spiders to capture woodlice efficiently, the functions of modifications remain unclear.

We consider three hypotheses. (1) Variation in cheliceral morphology is related to whether or not the *Dysdera* species feeds primarily on woodlice. (2) Variation in cheliceral morphology is related to different *Dysdera* species feeding primarily on different types of woodlice. (3) Variation in cheliceral morphology is related to *Dysdera* species adopting different prey-capture and prey-handling behaviour.

Materials and methods

Assessment of capture frequency

Two experiments were designed to compare, over a range of prey types, the capture frequencies of five *Dysdera* species, each species being a representative of a different type of cheliceral morphology (Table 1, Fig. 1). The first experiment was designed to determine the range of prey taken by each species. Ten adults of each *Dysdera* species were placed singly in Petri dishes (diameter 30 mm) with a moistened filter paper covering the bottom of the dish. For 2 weeks, the individuals were maintained at 20°C and deprived of prey. In preliminary experiments, we found that 2 weeks without food is an optimal period for ensuring that spiders are responsive to prey in the experiments (M. Řezáč, unpubl. data). Then, each spider was offered a single ground-dwelling arthropod of a type that is abundant in the dry forest habitats of the studied *Dysdera* species. In particular, we used woodlice [*Armadillidium vulgare* (Latreille, 1804)], centipedes (*Lithobius* sp.), millipedes (Julidae), ants [*Lasius niger* (Linnaeus, 1758)], beetles (various Carabidae), lycosid spiders (*Pardosa* sp.), earwigs (*Forficula auricularia* Linnaeus, 1758) and springtails (large Entomobryidae). We also offered them a few non-epigaeic arthropods, namely true bugs (various Miridae), flies (*Musca domestica* Linnaeus, 1758 or *Drosophila melanogaster* Meigen, 1830) and moths (*Ephestia küehniella* Zeller, 1879). All prey offered were alive and given one at a time. The order of prey presentation was random. The prey size was half to equal to the body length of the spider. If the prey was not captured within 30 min after being offered, it was replaced by another prey item chosen randomly until a prey item was accepted. We prevented the spiders from consuming the prey in order to keep them hungry. The records from the days when spiders did not accept any prey were not used for the analysis.

In the second experiment, we tested the choice of *Dysdera* species for two woodlice species with different defence tactics versus alternative prey. As prey we used a rolling woodlouse *A. vulgare*, a clinging woodlouse *Porcellio scaber* and, as an alternative prey, *M. domestica*. We used 50 individuals of each *Dysdera* species. The length of the

Table 1 *Dysdera* species used in this study, with a description of cheliceral characters

Species	Locality	Chelicerae
Dysdera sp. n.[a]	Israel: Mt Meron	'Unmodified': both basal segment (BS/carapace = 0.34) and fang (F/carapace = 0.41) short and robust (Fig. 1a and b)
Dysdera erythrina (Walckenaer, 1802)	Czech Republic: Prague	'Slightly elongated': both basal segment (BS/carapace = 0.47) and fang (F/carapace = 0.45) slightly elongated (Fig. 1c and d)
Dysdera abdominalis (Deeleman-Reinhold, 1988)[b]	Israel: Bet Guvrin	'Very elongated': both basal segment (BS/carapace = 0.72) and fang (F/carapace = 0.55) very elongated (Fig. 1e and f)
Dysdera spinicrus Simon, 1882	Israel: Mt Meron	'Concave': basal segment dorsally concave, fang elongated (F/carapace = 0.41), protruding forwards when opened (Fig. 1g and h)
Dysdera dubrovninnii Deeleman-Reinhold, 1988	Slovakia: Humenné	'Flattened': basal segment short (BS/carapace = 0.19), fang dorsoventrally flattened (Fig. 1i and j)

[a] Undescribed species related to *Dysdera dentichelis* Simon, 1882 (M. Řezáč, unpubl. data).

[b] Platnick (2007) presents this species as a representative of the genus *Tedia* Simon, 1882. However, according to molecular phylogeny, *Tedia* is an ingroup of the genus *Dysdera* (M. A. Arnedo, pers. comm.). Therefore, we propose the new combination *Dysdera abdominalis*.

prey corresponded approximately to the length of the spider's prosoma. Each Petri dish (with the same size as in the previous experiment) had a piece of moistened filter paper attached to the bottom to provide humidity. The three prey types were offered simultaneously to each *Dysdera* individual. After 24 h, we checked the dishes and recorded all cases in which only one prey was eaten. This was determined by inspecting whether the prey had been sucked out. *Dysdera* individuals that killed a prey but did not eat it or killed and consumed more prey were offered all three prey types again, and the dish was checked 24 h later. The chosen prey was the one that had been killed exclusively and consumed.

Data were analysed in R with generalized linear models (R Development Core Team, 2004). As all data were proportions, a binomial error structure with canonical link function was used (GLM-b). The maximal model of the two-way analysis of deviance (ANODEV), including the interaction between *Dysdera* species and prey species, was simplified by combining *Dysdera* species with a similar response. Each simplification was tested with χ^2 statistics. Combining continued until a minimal adequate model was achieved (Crawley, 2002). This procedure is in accordance with the principle of parsimony. Differences at treatment level (i.e. species) were then tested using *posterior* treatment contrasts.

Observation of predatory behaviour

For comparing the predatory behaviour of the different *Dysdera* species, we used the woodlouse *A. vulgare* as prey because we had determined that this species was generally accepted by the different *Dysdera* species. The prey size was half to equal to the body length of the spider. We recorded on video 20 attacks by each *Dysdera* species, each time performed by different individuals. Data came from both sexes and various ontogenetic stages for each *Dysdera* species. As before, the spiders were starved for 2 weeks before the test. The test duration was 2 h, but four of the five *Dysdera* species attacked immediately after encountering the prey. We focused on the role of the chelicerae in grasping the woodlouse. Grasping behaviour was represented in drawings based on frame-by-frame analysis of video sequences.

Results

Capture frequency

We found a significant difference in the capture frequency between species with unmodified and modified chelicerae (ANODEV, GLM-b, $\chi^2_{10} = 97$, $P < 0.0001$). The one species we tested that had unmodified chelicerae readily captured rather small, mainly soft-bodied arthropods such as flies, spiders, centipedes, moths and springtails (Fig. 2), and they never captured woodlice. All four species with modified chelicerae showed similar capture frequency for prey (simplification, $\chi^2_{22} = 20.8$, $P = 0.53$). Each of these species readily captured woodlice. For the species with very elongate chelicerae, woodlice were the only prey accepted.

In the second experiment, the relative capture frequencies with the different prey (flies, clinging woodlice and rolling woodlice) differed significantly among the five *Dysdera* species (ANODEV, GLM-b, $\chi^2_4 = 135.3$, $P < 0.0001$). Only the species with unmodified chelicerae captured flies more frequently than either of the woodlice (contrast, $\chi^2_2 = 66.4$, $P < 0.0001$, Fig. 3). In comparison with all other species, the species with very elongated and the species with flattened chelicerae captured significantly more rolling than clinging woodlice or flies (contrast, $\chi^2_2 = 69.5$, $P < 0.0001$).

Predatory behaviour

The species with unmodified chelicerae, *Dysdera* sp. n., attacked all prey types using a standard attack tactic ($n = 20$): both chelicerae grasped the prey synchronously from above. *Dysdera* sp. n. did not capture woodlice. In contrast, the other four species with modified chelicerae captured woodlice quickly and effectively, and the prey was

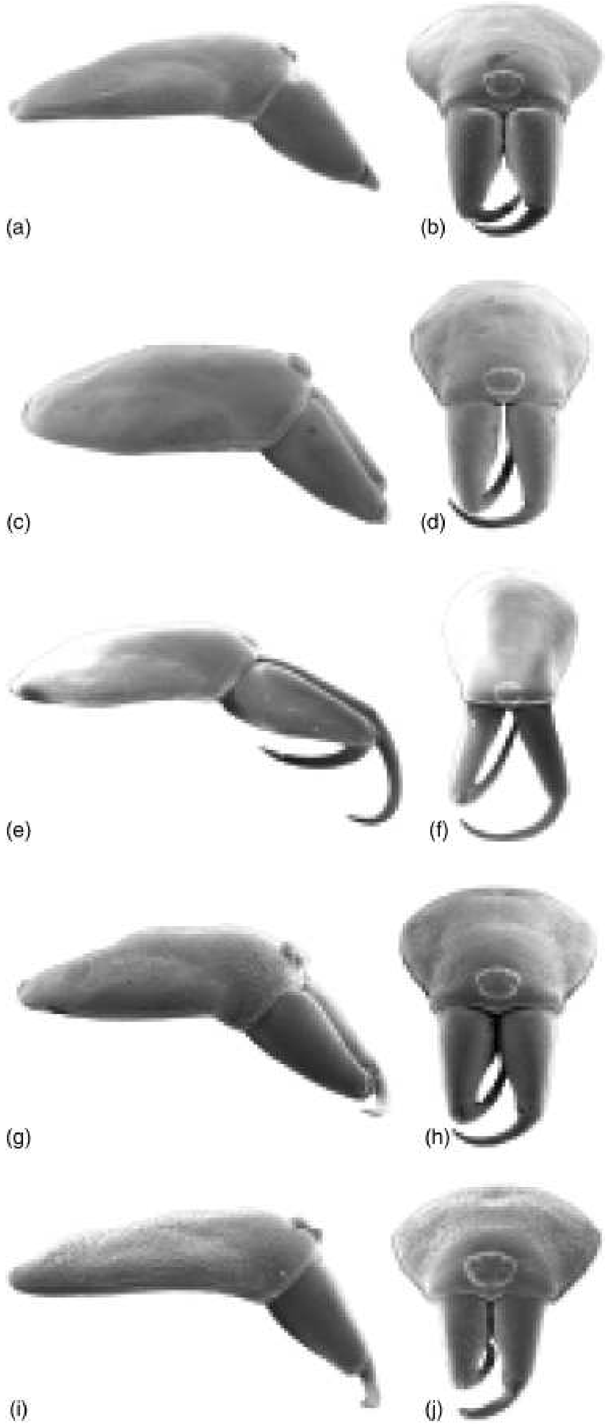

Figure 1 Chelicerae of the studied *Dysdera* spiders: (a, b) unmodified chelicerae, *Dysdera* sp. n.; (c, d) slightly elongated chelicerae, *Dysdera erythrina*; (e, f) very elongated chelicerae, *Dysdera abdominalis*; (g, h) concave chelicerae, *Dysdera spinicrus*; (i, j) flattened chelicerae, *Dysdera dubrovninnii*. (a, c, e, g, i) lateral view; (b, d, f, h, j) frontal view.

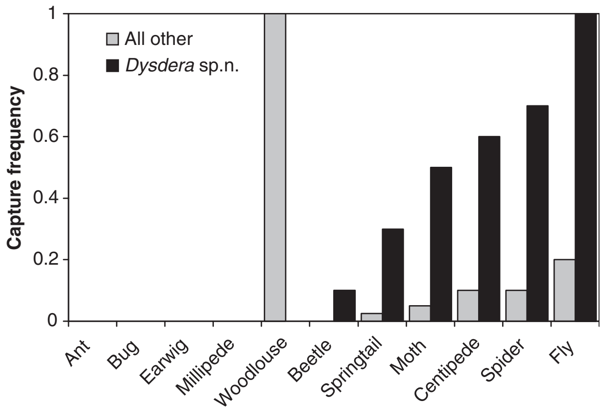

Figure 2 Proportion of 11 arthropod taxa accepted as prey by five *Dysdera* species tested (for each species, $n=10$).

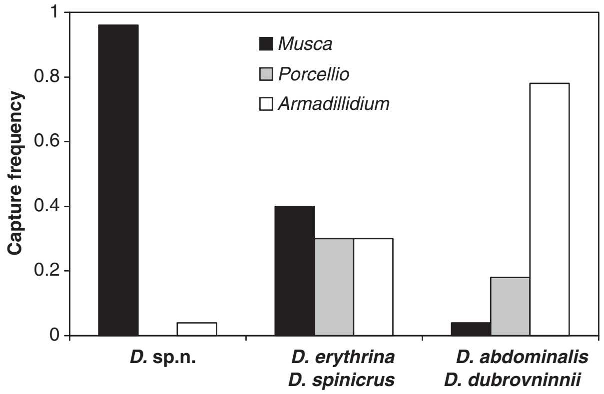

Figure 3 Capture frequency of five *Dysdera* species for three prey species (for each species $n=50$).

paralysed quickly. They used one of three grasping tactics depending on the particular way the chelicerae were modified.

Pincers tactic

This tactic was used exclusively by the two species with elongated chelicerae: *D. erythrina* (100%, $n=20$) and *Dysdera abdominalis* (100%, $n=20$). Both these species approached slowly, very close to the woodlouse, turned the prosoma sideways (i.e. one side moved up and the other moved down), enabling the spider to insert one chelicera underneath the woodlouse and the other over the dorsal side of the woodlouse (Fig. 4a). Then the spider gripped the woodlouse rapidly. While the fang of the lower chelicera penetrated the soft ventral side, the upper chelicera did not penetrate the hard dorsal side. The position of the upper chelicerae differed for the two species. In *D. erythrina*, the fang of the upper chelicera was usually erected, while in *D. abdominalis* it was folded in the cheliceral groove. Spiders used the left and right chelicera about equally often for

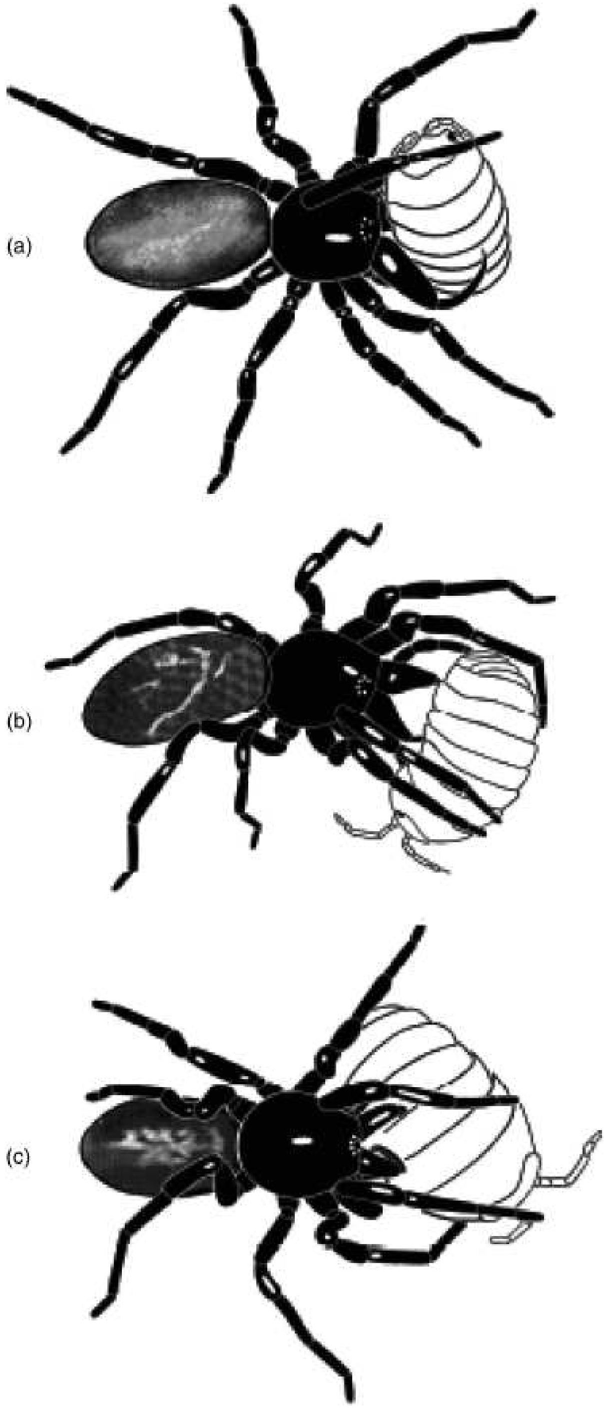

Figure 4 Grasping tactics used by *Dysdera* spiders to capture woodlice: (a) 'pincer' tactic of the *Dysdera* species with elongated chelicerae; (b) 'fork' tactic of the *Dysdera* species with concave chelicerae; and (c) 'key' tactic of the *Dysdera* species with flattened chelicerae.

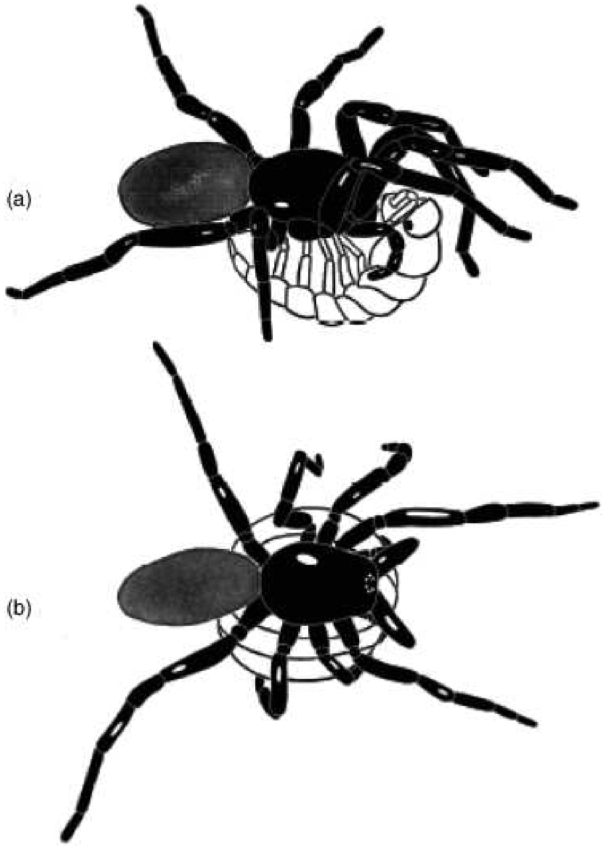

Figure 5 Grasp used for transportation of attacked woodlouse *Armadillidium vulgare* by (a) *Dysdera dubrovninnii* and (b) *Dysdera abdominalis*.

the attack. As the insertion of the lower fang was the first sudden motion of the attacking spider, the woodlouse usually did not have time to defend itself by rolling up. If it managed to roll up, spiders would wait motionless for less than a minute, with chelicerae ready for attack, for the woodlouse to unroll again. Alternatively, they rotated a woodlouse with their front legs and pedipalps and actively searched with one fang for an interstice between the sclerites. We observed this alternative tactic also in species using other grasping tactics. The spiders transported paralysed woodlice by holding the prey with chelicerae inserted into the ventral side of the head (Fig. 5a). The spiders did not chew the woodlice but sucked them out, leaving intact carcasses. This mode of transport and consumption was also used by *Dysdera spinicrus* and *Dysdera dubrovninnii*.

Dysdera abdominalis gently tapped the woodlouse with its front legs before an attack. This tapping behaviour did not induce the woodlouse to roll up, suggesting that it is soothing to the prey. The fang penetration was quick and the spider then retreated before the woodlouse could finish defensive rolling. The spiders transported paralysed woodlice by holding the prey with scopulae hairs on the tarsi and metatarsi of legs and pedipalps (Fig. 5b).

Fork tactic

This tactic was used exclusively by the species with concave chelicerae: *D. spinnicrus* (100%, $n = 20$). The spider slowly approached the woodlouse and stopped when about a half-body length away. The spider attacked abruptly by grasping the woodlouse with its forelegs, placing the chelicerae under the woodlouse and inserting its fangs into the soft ventral side (Fig. 4b). This occurred before the woodlouse could roll up. About 50% of the attacks were directed towards the head. The concave shape of the dorsal side of the basal cheliceral segment helped to get beneath the ventral side of woodlouse in a movement similar to scooping with a fork.

Key tactic

This tactic was used exclusively by the species with flattened chelicerae: *D. dubrovninnii* (100%, $n = 20$). The spider approached a woodlouse, searched with one fang for an edge of some sclerite on woodlouse's dorsal side and then slid the fang under the sclerite (Fig. 4c). The fangs are able to penetrate between sclerites only because they are both flat and dorsoventrally relatively elastic. Neither rolling nor clinging to the substrate provided protection against this tactic. Spiders could use either chelicera for the insertion. We called this the 'key tactic' as it reminded us of the skilful opening of a closed safe using a key.

Discussion

Our findings suggest that each of our three hypotheses helps explain variation in the cheliceral morphology of *Dysdera*. The species with unmodified chelicerae, *Dysdera* sp. n., used capture behaviour similar to spiders with generalized diets. *Dysdera* sp. n. readily captured a variety of arthropods, but never captured woodlice. In nature, we observed it feeding on a staphylinid beetle and on a heterospecific individual from the genus *Dysdera* (M. Řezáč, unpubl. data). In contrast to this, all the species with modified chelicerae readily captured woodlice. However, species with chelicerae modified in different ways used different grasping tactics when preying on woodlice.

The two species with elongated chelicerae, *D. erythrina* and *D. abdominalis*, penetrated the soft ventral side of woodlouse with one chelicera and held but did not penetrate the dorsal side of woodlouse with the other one. We predict these two *Dysdera* species to capture mainly clumsy rollers (*sensu* Schmalfuss, 1984). Capturing more agile, faster-moving woodlice might be difficult for these *Dysdera* species because accurate directing of the fang to the ventral side of the woodlouse requires getting closer than agile, fast-moving woodlice normally allow before running away.

The concave shape of the dorsal side of its chelicerae allowed *D. spinicrus* to tuck its chelicerae under a woodlouse and consequently bite into the ventral side. This is a quick attack without previous contact, which should be effective even for clingers, which are able to quickly find a substrate to cling onto.

As flattening the chelicerae allowed *D. dubrovninnii* to insert its fang between the sclerites on the dorsal side of a woodlouse, rolling and clinging, which shield the soft ventral side of the woodlouse's body, seem to be ineffective defences against *D. dubrovninnii*.

These different cheliceral modifications and capture tactics enabled *Dysdera* spiders to overcome the unusual defence tactics of woodlice – heavy armour protecting most of their body and behavioural defences protecting their soft ventral side.

Except for *D. abdominalis*, the *Dysdera* species we tested carried their prey by holding them in their chelicerae. *Dysdera abdominalis*, however, used an unusual method of transporting woodlice by dragging them using apical leg and pedipalp segments equipped with scopulae. We suggest that the extreme elongation of the chelicerae in this species makes the transport of prey using the chelicerae less efficient. Thus, a modification that increases the efficiency of the attack may have constrained the transport, resulting in an evolutionary shift in the mode of transport. Similar instances of constraints on prey capture in spiders resulting from changes in morphology have been studied mainly in the context of sexually selected traits, and are thus restricted to one sex. For example, extreme elongation of male chelicerae in some salticids severely restricts their use for prey capture (Pollard, 1994).

The results of capture frequencies suggest that there are three main groups of prey specificity in *Dysdera*: (1) non-woodlice eating species that have unmodified chelicerae, (2) facultative woodlice specialists that have chelicerae that are moderately modified (3) species that seem to be at least close to obligatory woodlice specialists that have chelicerae with extreme modifications. As the features of the chelicerae vary over a continuum (e.g. Deeleman-Reinhold & Deeleman, 1988), the strength of preference might also do so. The prey generalist, *Dysdera* sp. n., refused woodlice. Facultative woodlice specialists, *D. erythrina* and *D. spinicrus*, captured other prey besides woodlice and were not choosy with regard to the type of woodlouse. These species are presumed to capture mainly woodlice in nature (Řezáč & Pekár, 2007). *Dysdera crocata*, possessing elongated chelicerae, seems to belong to this category. It was observed in the laboratory to eat almost all prey that was sufficiently small and slow moving (Cooke, 1965*a–c*) and Pollard *et al.* (1995) failed to document a preference for woodlice in laboratory experiments. This species might be ecologically plastic, it is the only species of the family Dysderidae that has colonized most parts of the world (Cooke, 1967). The species that seem to be at least close to obligatory woodlouse specialists, represented by *D. abdominalis* and *D. dubrovninnii*, captured virtually only woodlice; moreover, they captured rollers significantly more frequently than clingers.

To our knowledge, *Dysdera* spiders are the only specialized woodlice predators occurring outside tropical zones. With the striking variability of morphological adaptations and grasping tactics described here, these spiders are a highly diversified clade of oniscophagous feeders.

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