Diaspores of myrmecochorous plants as food for certain spiders

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Abstract. Spiders eating diaspores (seeds and fruits) from myrmecochorous plants – i.e. those adapted to distribution by ants – is recorded here for the first time as a new case of herbivory in these typical predators. Having found seeds of *Costus dubius* (Afzel.) K. Schum. (1904) trapped in the web of a *Parasteatoda* spider (Theridiidae), tests with available myrmecochorous seeds and spiders in the greenhouses of the Botanical garden of the P. J. Šafárik University in Košice (Slovakia) were carried out. *Parasteatoda* spiders can actively collect *C. dubius* seeds near their webs and feed on them for a long time. Diaspores with elaiosomes (nutrient-rich appendages) from five other myrmecochorous plant species thrown directly into webs of *Parasteatoda* sp. and *Uloborus plumipes* Lucas, 1846 (Uloboridae), another spider species very abundant at this location, were also consumed. These initial observations show that the special chemical composition of elaiosomes, which imitates insect prey primarily for ants, can be attractive for some spider species too. Considering the tested taxa, in the case of Uloboridae contact with such food sources is improbable in their typical niches. However, at least some Theridiidae could also consume myrmecochorous diaspores in nature, especially if they are near source plants or paths of ants transporting these diaspores.

Keywords: Araneae, elaiosomes, herbivory, myrmecochory, *Parasteatoda*, *Uloborus plumipes*

Zusammenfassung. Diasporen von Pflanzen mit Myrmekochorie als Nahrung für manche Spinnen. Als neuer Fall von Herbivorie durch typischerweise räuberische Spinnen wird erstmals belegt, dass Spinnen Diasporen (Samen und Früchte) von Pflanzen mit Myrmekochorie (Ameisenausbreitung) fressen. Als Samen von *Costus dubius* (Afzel.) K. Schum. (1904) im Netz von *Parasteatoda*-Arten (Theridiidae) gefunden wurden, wurden Test mit verfügbaren Samen von Pflanzen mit Myrmekochorie und Spinnen in den Gewächshäusern des Botanischen Gartens der P.J. Šafárik Universität in Košice (Slowakei) durchgeführt. Es konnte bestätigt werden, dass *Parasteatoda*-Arten aktiv Samen von *C. dubius* in der Nähe iher Netze sammeln und sich davon über längere Zeit ernähren können. Diasporen mit Elaiosomen (energiereiche Anhängsel, „Ölkörperchen") fünf weiterer Pflanzenarten mit Myrmekochorie, die direkt in die Netze von *Parasteatoda* sp. und von *Uloborus plumipes* Lucas, 1846 (Uloboridae) gegeben wurden – letztere Art kam ebenfalls sehr häufig vor, wurden ebenfalls gefressen. Diese ersten Beobachtungen zeigen, dass die besondere chemische Zusammensetzung der Elaiosomen, die primär Insektennahrung für Ameisen imitieren, auch attraktiv für manche Spinnenarten sein können. Im Fall der untersuchten Uloboridae ist ein Kontakt mit solcher Nahrung in ihrem typischen Lebensraum unwahrscheinlich. Aber mindestens einige Theridiidae-Arten könnten in ihrem natürlichen Lebensraum Diasporen von Pflanzen mit Myrmekochorie ebenfalls fressen, insbesondere in der Nähe der Pflanzen oder von Ameisenstraßen, wo solche Diasporen transportiert werden.

Spiders are primarily known as predators, mainly feeding on small invertebrates. An exception is *Bagheera kiplingi* Peckham & Peckham, 1896 (Salticidae) which largely feeds on plant products (Beltian bodies and foliar nectar) from acacias (*Vachellia* sp.) (Meehan et al. 2009). Some other spiders ocassionally supplement their diet with plant resources. Nyffeler et al. (2016) summarised 95 known incidents of spiders feeding on plants; mostly under natural conditions. In their review, plant resources used by spiders were divided into six main groups: 1. leaves (Beltian and Müllerian bodies, plant sap), 2. sugar solutions (floral and extrafloral nectar, honeydew as a plant-derived sugary fluid, stigmatic exudates), 3. pollen, 4. seeds, 5. spores and 6. plant material present in the guts of herbivorous prey. Among these cases, seed feeding by spiders consisted of only two reports. First, an orb-weaving spider, *Neoscona adianta* (Walckenaer, 1802) (Araneidae), was observed sucking a grass seed (Poaceae) (Berland 1933). Second, it was assumed by Nyffeler et al. (2016) that tiny airborne plant seeds trapped in spider webs become unintentionally ingested along with the old threads during the recycling process. Furthermore, raising spiders on a liquid diet made from the seeds of *Glycine max* (L.) Merr., 1917 (Fabaceae) under laboratory conditions was reported by Amalin et al. (1999, 2001).

Due to the above mentioned scarcity of reports of spiders feeding on plants, and especially on seeds, it was a surprise to see (on 5.I.2018) two relatively heavy seeds of *Costus dubius* (Afzel.) K. Schum. (1904) (Costaceae) in the web of a *Parasteatoda* (Theridiidae) above the inner sill of a greenhouse window in the Botanical Garden of the P. J. Šafárik University in Košice (hereinafter BG PJŠU). About three weeks before (12.XII.2017), the seeds of *C. dubius* were intentionally scattered here to observe their transport by local ants (especially *Lasius* sp.). While preparing a study on ants in greenhouses many seeds remained on the window sill. The question was whether some seeds later enetered the spider's web randomly or whether this spider actually pulled them up as a food. In the second option, it would be interesting to see whether diaspores of this type (seeds or fruits with elaiosomes) could also be used by other spiders.

Myrmecochory is a phenomenon more or less widespread all over the world, in which diaspores of myrmecochorous plant species are adapted for distribution by ants. Such diaspores are usually equipped with elaiosomes: appendages of specific composition, rich mainly in proteins and fatty acids. According to Lengyel et al. (2010), the number of myrmecochorous plant species can be estimated to be at least 11000 in 77 families and according to World Spider Catalog (2018), there are 47904 accepted spider species in 117 families. To date, consumption of such seeds or fruits by spiders has not been reported.

Material and methods

More than 4000 higher plant taxa are registered in the BG PJŠU (48.735°N, 21.238°E, 220–370 m a.s.l.), about 2500 of them from tropical and subtropical areas growing in heated greenhouses (Mártonfiová et al. 2010). Adaptations for myrmecochory are known for about 300 species but in fact diaspores were disposable only from one tropical species, *Costus*

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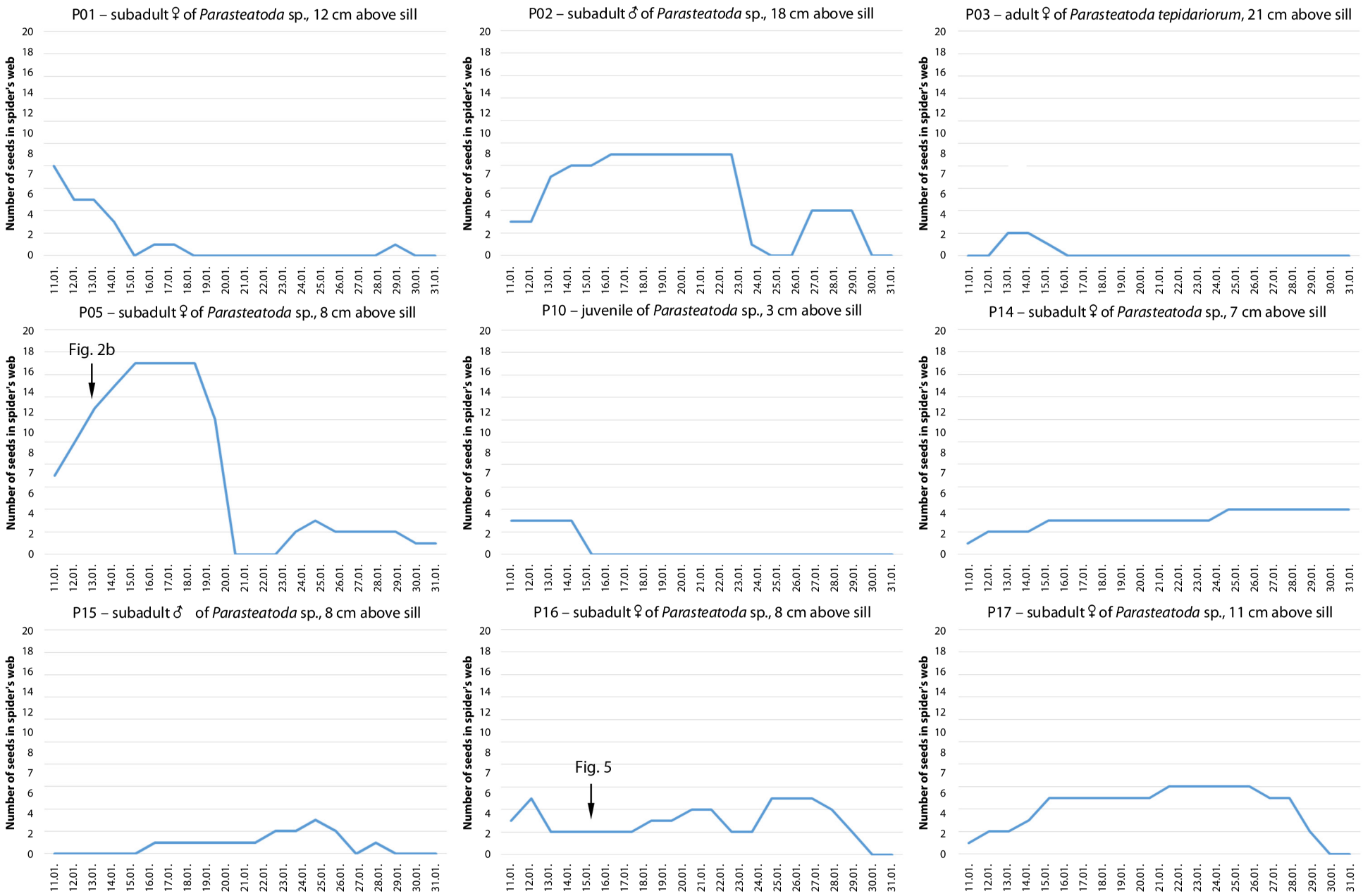

Fig. 1: Number of seeds of *Costus dubius* in the webs (in the air above underlay) of the selected nine spiders *Parasteatoda* sp. (P01–P17) each day (1.–20., 11.–31.I.18, except 28.I.18) during checking time. Initially (day 0, 10.I.18) 20 seeds were put on the window sill inside the greenhouses of BG PJŠU below the spiders. In the following days some seeds were pulled up or later dropped from the web by the spiders.

dubius from West Africa, and from five species of European temperate regions: *Chelidonium majus* L. (1753), *Corydalis solida* (L. 1753) Clairv. 1811 (Papaveraceae), *Galanthus nivalis* L. (1753) (Amaryllidaceae), *Asarum europaeum* L. (1753) (Aristolochiaceae) and *Hepatica nobilis* Schreb. 1771 (Ranunculaceae).

The arachnofauna of heated greenhouses in the BG PJŠU comprises 62 spider taxa in 21 families (Šestáková et al. 2017). *Parasteatoda tepidariorum* (C. L. Koch, 1841) (Theridiidae) and *Uloborus plumipes* Lucas, 1846 (Uloboridae) are the most abundant spider species here and were confronted with the diaspores of myrmecochorous plants mentioned above. As the syntopic *P. tepidariorum* and *Parasteatoda tabulata* (Levi, 1980) are barely distinguishable in their webs, they are usually referred together here as *Parasteatoda* sp. in this paper.

Some spiders, especially cobweb spiders (Theridiidae), reside in the same place for a long time. Seventeen such sites with spider individuals (coded as P01–P17) were selected along inner sides of greenhouses. Below each selected spider, 20 seeds of *Costus dubius* were placed on the sill, trying not to touch nearby sticky threads anchored to the sill (Fig. 2a). In the following 20 days the number of seeds picked up was checked (once a day, usually around midday). Only nine *Parasteatoda* who stayed for the full 20 days at the same site (others disappeared in the meantime) were included in the final evaluation (Fig. 1, 2).

Fig. 2: A *Parasteatoda* sp. (in red circle) with the code P05 (see text and Fig. 1 for other details) with the seeds of *Costus dubius* (in blue circles) in a greenhouse of BG PJŠU. **a.** 20 seeds put on the sill below spider (10.I.2018) at the beginning of the test; **b.** Three days later (13.I.2018), 13 seeds were pulled up from the sill by this spider; **c.** Detail of the spider with some of the pulled up seeds (11.I.2018); **d.** Detail of the spider feeding on one of the seeds (15.I.2018)

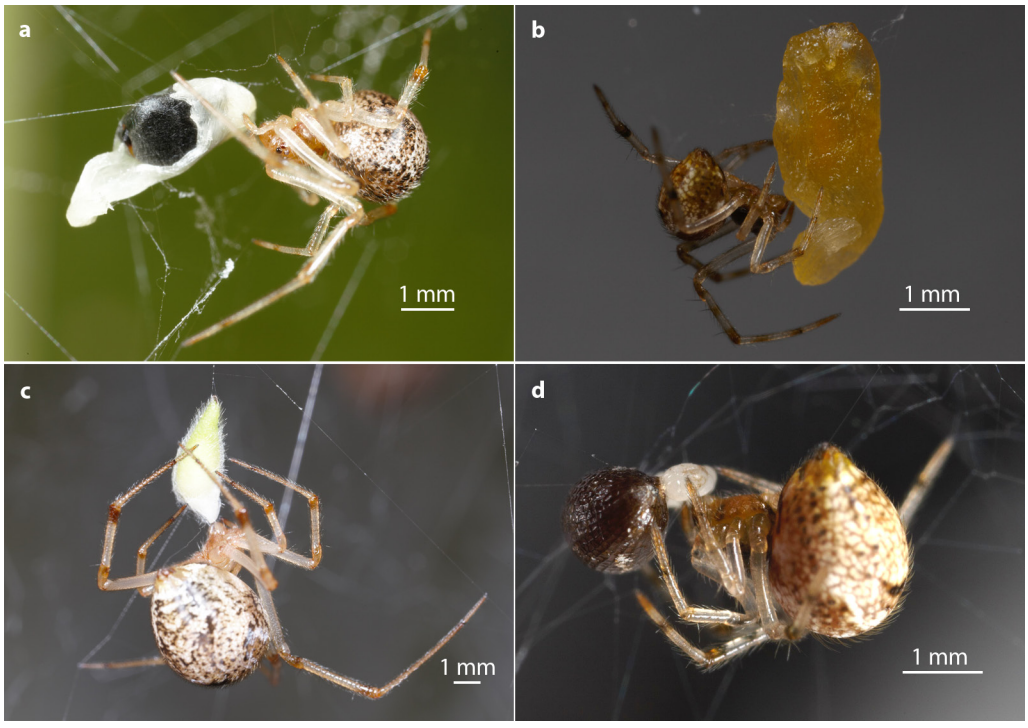

Fig. 3: Different individuals of *Parasteatoda* sp. with the diaspores of: **a.** *Costus dubius*; **b.** *Galanthus nivalis*; **c.** *Hepatica nobilis*; **d.** *Chelidonium majus*

Additional observations were made on several other individuals of *Parasteatoda* and *Uloborus plumipes* to assess their responses when disposable myrmecochorous diaspores were thrown directly into their webs.

Additional tests offering seeds of *Costus dubius* as potential food were conducted with *Pholcus* sp. (Pholcidae), *Agelena labyrinthica* (Clerck, 1757) (Agelenidae), *Hasarius adansoni* (Audouin, 1826) (Salticidae) and *Mangora acalypha* (Walckenaer, 1802) (Araneidae).

Results

Parasteatoda (Theridiidae) can actively collect myrmecochorous diaspores (*Costus dubius*) in the vicinity of their webs

Some seeds of *C. dubius* were pulled up from the sill by spiders and other seeds were thrown out from the web (Fig. 1). Usually the picked up seeds remained in the web long enough for counting once a day. A possible source of error could be ants carrying the seeds away from below the spiders. Nevertheless, the results show the ability of *Parasteatoda* sp. spiders to find the seeds in the vicinity of their webs, pull them up and consume them (Fig. 2). In the humid conditions of greenhouses, the attractive properties of the selected seeds with their elaiosomes were preserved for at least three weeks after their separation from mother plants (Fig. 1).

Selected myrmecochorous diaspores placed directly into the webs of *Parasteatoda* sp. and *Uloborus plumipes* were consumed in most cases

Myrmecochorous diaspores from different plants were placed into the webs of five *Parasteatoda* sp. (1× *C. dubius*, 1× *G. nivalis*, 2× *H. nobilis* and 1× *C. majus*) and 24 *U. plumipes* (3× *A. europaeum*, 4× *C. dubius*, 5× *C. solida*, 1× *G. nivalis*, 4× *H. nobilis* and 7× *C. majus*). Times between putting a seed into the web and the approach of a spider to the potential food source varied. Especially in the case of *U. plumipes* a seed may not be touched for several hours. However, sooner or later, the diaspores of all tested myrmecochorous plants were eaten (Fig. 3, 4). Only one subadult female of *U. plumipes* threw out three seeds of *C. majus* from its web shortly after finding them, probably without initial feeding. In all other cases seed eating took minutes to hours. Sometimes seeds were first wrapped with silk (Fig. 4c) just like in real prey capture.

Tests with other spider species

Some other, less common spider species were also offered seeds of *C. dubius* as potential food. These additional tests included the following spider species: *Pholcus* sp. (n = 5), *Mangora acalypha* (n = 1), *Agelena labyrinthica* (n = 1) and *Hasarius adansoni* (n = 3). None of the tested spiders was observed feeding on seeds. However, when three seeds were put into

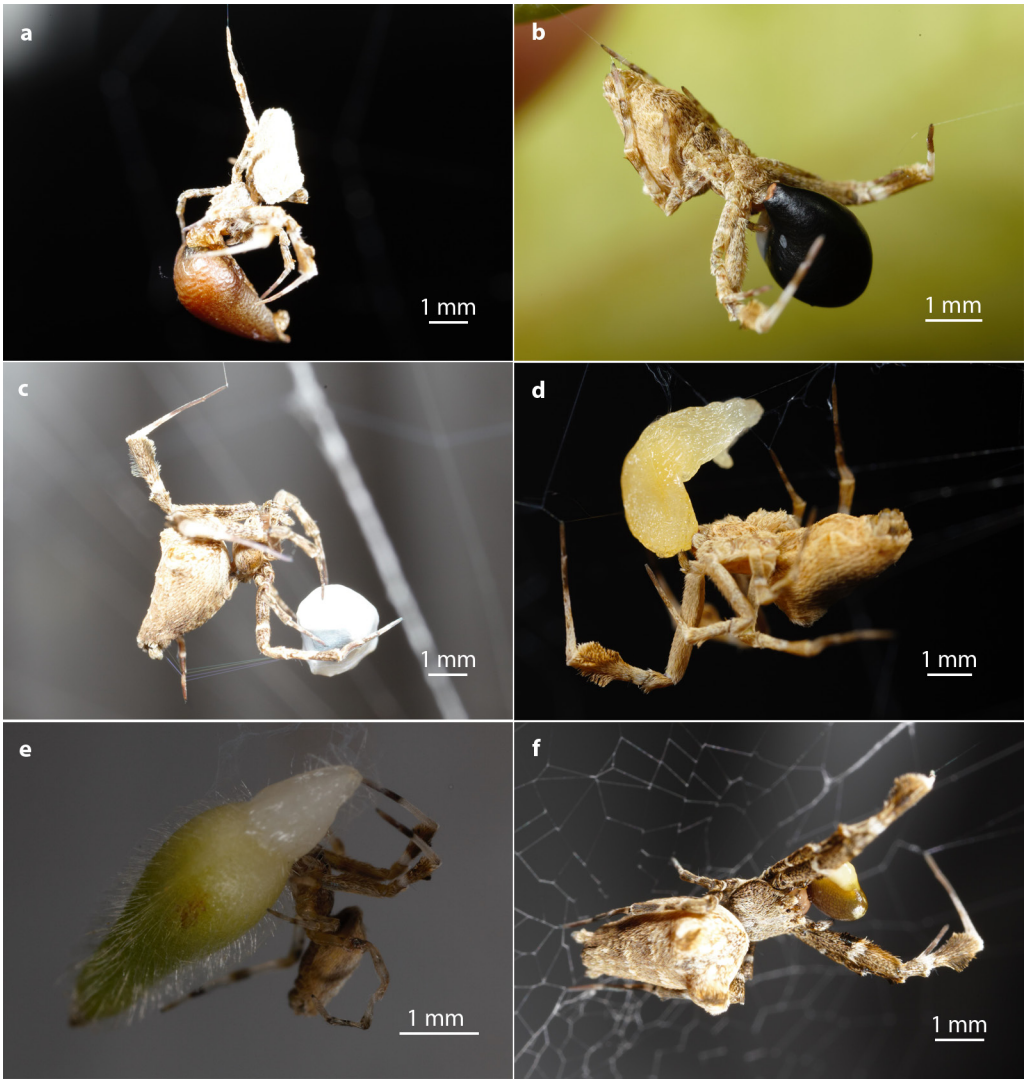

Fig. 4: Different individuals of *Uloborus plumipes* with diaspores of: **a.** *Asarum europaeum*; **b.** *Corydalis solida*; **c.** *Costus dubius*; **d.** *Galanthus nivalis*; **e.** *Hepatica nobilis*; **f.** *Chelidonium majus*

Fig. 5: Simultaneous occurrence of two seeds of *Costus dubius* and a worker of *Lasius brunneus* in the web of *Parasteatoda* sp. spider with the code P16, 15.I.2018 (see text and Fig. 1 for other details), above sill in a greenhouse of BG PJŠU. In this case the prey was captured by a resident spider after an ant worker was coming here, either accidentally or attracted to the intentionally placed seeds (by the experimentator) on the sill (and, previously, some seeds were picked up by a spider). Under natural conditions the opposite situation may be more likely – seeds could be brought below spider web by ants themeselves and afterwards (after the killing ants) these seeds could be pulled up by the spiders.

the periphery of the web of *Agelena labyrinthica*, all of them were found closer to the center after 3–4 days. Due to the small number of tested spider individuals, these observations are not necessarily conclusive, but they at least show a trend indicating that different spider species may differ in their propensity to consume myrmecochorous diaspores.

Discussion

Elaiosomes, as juicy or fleshy appendages of diaspores, can be formed from various tissues of seeds, fruits or even other plant parts. Their chemical composition is quite different from all other plant structures (Leins & Erbar 2010). According to Fisher et al. (2008), elaiosomes of 15 plant species from seven different families were more similar to each other than each was to the other seed parts of the same species. The high nutritional value of elaiosomes is related especially to fats and sugars, but they also contain proteins, vitamins and other substances (Leins & Erbar 2010). Some of these chemicals have signalling effects on ants. For example diglyceride 1,2-diolein, which is also a component of insect hemolymph, is supposed to be the main signalling compound for ants collecting diaspores with elaiosomes (Rico-Gray & Oliveira 2007). Even purely carnivorous ant species, which usually avoid plant resources, are attracted to elaiosomes whose composition is more similar to insects than other plant tissues (Hughes et al. 1994). This is probably the reason why some spiders, which are otherwise obligate predators, can consume myrmecochorous diaspores.

During plant evolution, elaiosomes appeared in many independent events after ants started to dominante terrestrial ecosystems (Dunn et al. 2007, Lengyel et al. 2010). It proved advantageous for many plant species to distribute themselves with the help of these omnipresent ant predators. Such plants evolved diaspores equipped with imitations of insect prey (elaiosomes as a reward for ants). This is usually a mutually advantageous relationship in which ants transport diaspores, utilise highly nutritional elaiosomes and leave the rest of diaspores untouched in more or less remote sites. Therefore myrmecochory could arise from exploitation of predator–prey relationships (Fenner & Thompson 2005). Formation of such structures by plants was 'targetted' towards omnivorous and carnivorous ants so that they would distribute diaspores, but other generalist predators such as some ground beetles (Ohara & Higashi 1987) can use this resource as well. Animals consuming elaiosomes without dispersing the seeds disrupt ant–plant mutualism (Rico-Gray & Oliveira 2007) and, as is shown in this paper, some spiders can be included – from an ecological point of view – in this disruptive group too.

As shown here, spiders can consume diaspores with elaiosomes. Another question is how widespread this phenomenon is in the natural environment? In the case of Uloboridae it does not probably occur, because such diaspores would rarely get into their webs. But in the case of Theridiidae, with threads attached to the ground, it is more probable. Especially when a web is constructed near the source plants, or above ant trials where diaspores are transported. Many Theridiidae species catch ants using sticky threads anchored to the substrate. Even in our greenhouses, individuals of all the common ant species [*Lasius niger* (Linnaeus, 1758), *Lasius brunneus* (Latreille, 1798), *Lasius emarginatus* (Olivier, 1792), *Camponotus fallax* (Nylander, 1856), *Tetramorium* sp.] were documented as prey of *P. tepidariorum* or *P. tabulata*. Workers of the same spectrum of ant species readily grab the myrmecochorous seeds on offer. In the context of the above findings, a spider could consume both a worker ant and the seed carried along and abandoned after attack. Direct observation of such activities is missing so far, but the simultaneous occurrence of seeds and ants in the web was registered (Fig. 5). Overall, it seems to be another example of tritrophic interactions between spiders, plants and ants. The possible interactions of some Theridiidae spiders with myrmecochorous plants and ants are not as specific as in the salticid *Bagheera kiplingi* on *Vachellia* sp. acacias with *Pseudomyrmex* sp. ants (Meehan et al. 2009).

Nyffeler et al. (2016) documented spiders feeding on plant materials representing about 20 different plant families. In the current paper, it is shown that spiders feed on plant materials representing five additional families (Amaryllidaceae, Aristolochiaceae, Costaceae, Papaveraceae and Ranunculaceae). Considering high number of other non-tested myrmecochorous plants and spiders, other families might be expected to supplement this list. On the one hand, there may be differences in detailed chemical composition of elaiosomes in individual plant species, on the other, there are various food strategies and preferences of spiders with different opportu-

nities to encounter such diaspores. Sanders (2013) assumed greater potential for interactions between plants and spiders, especially based on the wide range of spider families using nectar as supplementary resource. Another very widespread potential plant resource – diaspores with elaiosomes, in connection with preliminary observations described in this paper, show that herbivory in spiders may be more common than previously assumed.

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