

# Phytophagy in jumping spiders: The vegetarian side of a group of insectivorous predators

Martin Nyffeler<sup>1</sup>

<sup>1</sup> Section of Conservation Biology, Department of Environmental Sciences, University of Basel, Basel, Switzerland; *email*: martin.nyffeler@unibas.ch

**Abstract:** Jumping spiders (Salticidae), a group of predominantly insectivorous predators, occasionally supplement their insect prey by deriving nutrients from plant food ('facultative phytophagy'). The aim of this paper is to give a brief overview of the plant eating activities of salticids based on the published literature. Plant-eating by salticids has been reported from all continents except Antarctica and Europe. With regard to Antarctica it must be said that salticid spiders are absent from there. The previous lack of observations from Europe, on the other hand, may be explained by the fact that plant-eating by salticids is typically found in the warmer areas of the globe ( $\leq 40^\circ$  latitude) and because most of Europe is located in colder climates ( $> 40^\circ$  latitude), it comes as no big surprise that this type of feeding has not yet been detected in European salticids. In order to exploit plant food resources, salticid spiders have to overcome various hurdles. Firstly, plant products such as floral nectar and pollen, serving to attract pollinators, might be chemically protected to deter nectar robbers and pollen thieves. Defensive chemicals such as alkaloids and cardenolides, if ingested along with plant food, may alter the spiders' behavior as has been demonstrated in laboratory experiments with non-salticid spiders. Whether such behavior-altering chemicals have also an effect on free-living salticid spiders, remains to be researched. Secondly, plant-derived foods such as extrafloral nectar, Beltian bodies or coccid honeydew are aggressively defended by ant bodyguards and spiders must break through the ant defenses in order to get access to these types of food. Salticids detect ants by sight and are able to actively avoid them in most cases. Another situation does occur when the approaching salticid is an ant-mimic perceived by ants as ant (e.g., genus *Myrmarachne* or *Peckhamia*); ant-mimicking salticids appear to have unhindered access to plant-derived foods such as extrafloral nectar or coccid honeydew. Thirdly, spiders (adapted to eat insect prey) might require some specific enzymes enabling them to chemically break down plant materials. Currently it seems to be well understood how spiders accomplish the digestion of liquid plant food, whereas the process of digesting solid plant tissue is not yet completely investigated. As in other predaceous arthropods, the ability of spiders to derive nutrients from plant materials is broadening these animals' diet which may have survival value during periods of prey scarcity.

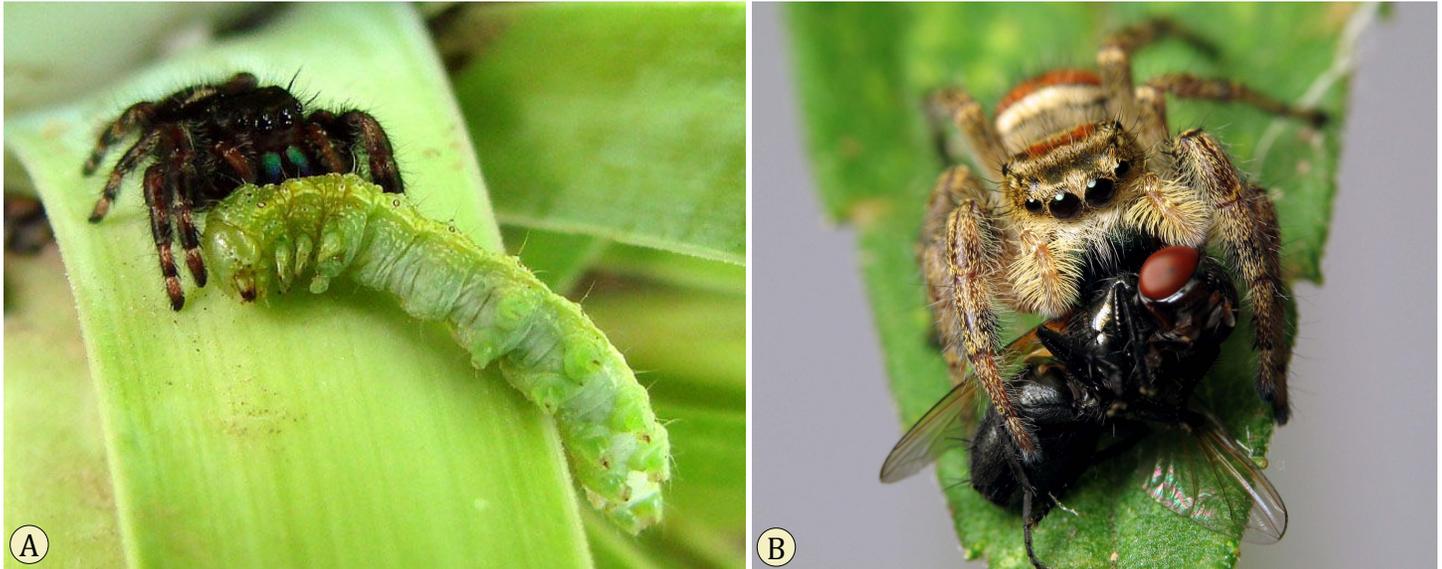
**Key words:** ant bodyguards, ant-mimics, defensive chemicals, facultative phytophagy, geographic distribution, plant food, Salticidae

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## Introduction

A large number of arthropod predators such as for instance ants (Formicidae), flower bugs (Anthocoridae), green lacewings (Chrysopidae), ground beetles (Carabidae), hoverflies (Syrphidae), ladybugs (Coccinellidae), milkweed bugs (Lygaeidae), and predatory mites (Phytoseiidae) supplement their insect prey by occasionally deriving nutrients from plant materials (Wäckers & Fadamiro 2005; Lundgren 2009). Such occasional consumption of plant food by predaceous arthropods is termed as 'facultative phytophagy' (see Armer *et al.* 1998). As Lundgren (2009) points out, a variety of plant-derived materials including honeydew, nectar, plant sap, pollen, seeds, and spores are utilized by predators as supplementary food. Even spiders, reputed to be the classical examples of insectivorous predators (Figure 1), are now acknowledged to include plant materials in their diets. In a recent review, Nyffeler *et al.* (2016) documented that spiders from at least 10 families occasionally feed on plant materials, with jumping spiders (Salticidae) being the dominant spider group engaged in this type of

feeding behavior (~60% of all reported incidents). As plant-inhabiting, highly mobile predators with excellent capabilities in detecting and locating static food (see Nyffeler *et al.* 1990), the salticids seem to be predestined among the spiders to include some plant materials in their diets. This publication aims to provide a short overview of the different types of plant-eating activities of the salticid family based on the literature and supported by photographic evidence. In the following it is distinguished between a) feeding on liquid plant food, and b) feeding on solid plant tissue.



**Figure 1.** A, *Phidippus audax* (Hentz, 1845) feeding on a noctuid caterpillar (Image credit: Lawrence Duhon, Fort Worth, Texas). B, Adult female *Phidippus clarus* Keyserling, 1885 feeding on a brachyceran fly (photo by David E. Hill, Simpsonville, South Carolina).

### Feeding on liquid plant food

Nectar – a sweet, sugary liquid – is produced by tens of thousands of plant species in special glands termed ‘nectaries’ (*e.g.*, Koptur 2005; Lundgren 2009; Joppa *et al.* 2011; Weber & Keeler 2013). There are two different groups of nectaries: 1) floral nectaries (located within flowers), and 2) extrafloral nectaries (located on leaves, petioles or stems). Although salticids have been reported drinking nectar from both floral and extrafloral nectaries, the consumption of extrafloral nectar seems to prevail (see Edmunds 1978; Douglas 1983; Ruhren & Handel 1999; Blüthgen & Reifenrath 2003; Cross & Jackson 2009; Hill 2011a; Soren & Chowdhury 2011; Kuja *et al.* 2012; Nahas *et al.* 2012; Hill & Edwards 2013; Mondal *et al.* 2013; Nyffeler *et al.* 2016). Not only in spiders, but also in many other arthropod predator taxa the consumption of extrafloral nectar is apparently prevailing over floral nectar (Lundgren 2009). Thus in the following, particular emphasis was placed on the consumption of extrafloral nectar. It is believed that chemical cues, both olfactory and gustatory, are used by spiders to detect and locate nectar sources (Taylor 2004; Patt & Pfannenstiel 2008, 2009; Cross & Jackson 2009). In their search for nectar the salticids wander over plants and stop for a while each time they have approached a nectary (Figures 2-3). The spiders then press their mouthparts into the nectary opening probing and/or imbibing nectar, which may last from a few seconds up to a few minutes (Nico Blüthgen, pers. comm.; David Hill, pers. comm.). Extrafloral nectar attracts ants in large numbers which aggressively defend the nectaries taking on the role of plant bodyguards, and spiders have first to break through these defenses to get access to nectar (Blüthgen & Reifenrath 2003; Soren & Chowdhury 2011). Equipped with excellent vision many salticids can detect ants by sight (Jackson *et al.* 2008a). An approaching salticid usually first observes from a

distance whether ants are present and waits until the ants depart, before rushing to a nectary (Figures 4-5; David Hill, pers. comm.). Should it still come to a spider-ant encounter, then a spider may temporarily retreat until the ant has passed by or it may run away (Soren & Chowdhury 2011; Nico Blüthgen, pers. comm.); salticids have the ability to outrun or out-jump ants if chased (Eric Olson, pers. comm.). Cases where ants were killed by salticids, however, are known as well (Douglas 1983). Indeed some salticids habitually feed on ants (Edwards *et al.* 1974; Jackson & Olphen 1991, 1992; Li *et al.* 1996; Jackson *et al.* 1998). Still another situation does occur when the spider approaching an extrafloral nectary is an ant-mimic (Figure 3F). In South Carolina, an ant-like salticid spider in the genus *Peckhamia* has been seen running from nectary to nectary, mimicking the behavior of ants (David Hill, pers. comm.). Such spiders, obviously perceived by ants as conspecifics, appear to face reduced aggression from ant bodyguards (Jackson & Willey 1994; Ceccarelli 2007; Jackson *et al.* 2008b; Uma *et al.* 2013). It is therefore no surprise that a large number of species of ant-like salticids (genera *Myrmarachne* and *Peckhamia*) are found on the list of nectarivorous spiders (see Jackson *et al.* 2001). In the literature the question was raised whether drinking nectar is done to actually obtain nourishment or whether it is merely done to satisfy the spiders' need for moisture (*e.g.*, Edmunds 1978). In laboratory choice tests salticids showed a distinct preference for artificial nectar (30% sucrose solution used as a nectar surrogate) compared to pure water (Ruhren & Handel 1999). These experiments indicate that under natural conditions salticids drink nectar to obtain nutrients in addition to moisture (Jackson *et al.* 2001). Nectarivory in salticids has been shown to be a phenomenon occurring in many regions of the globe.



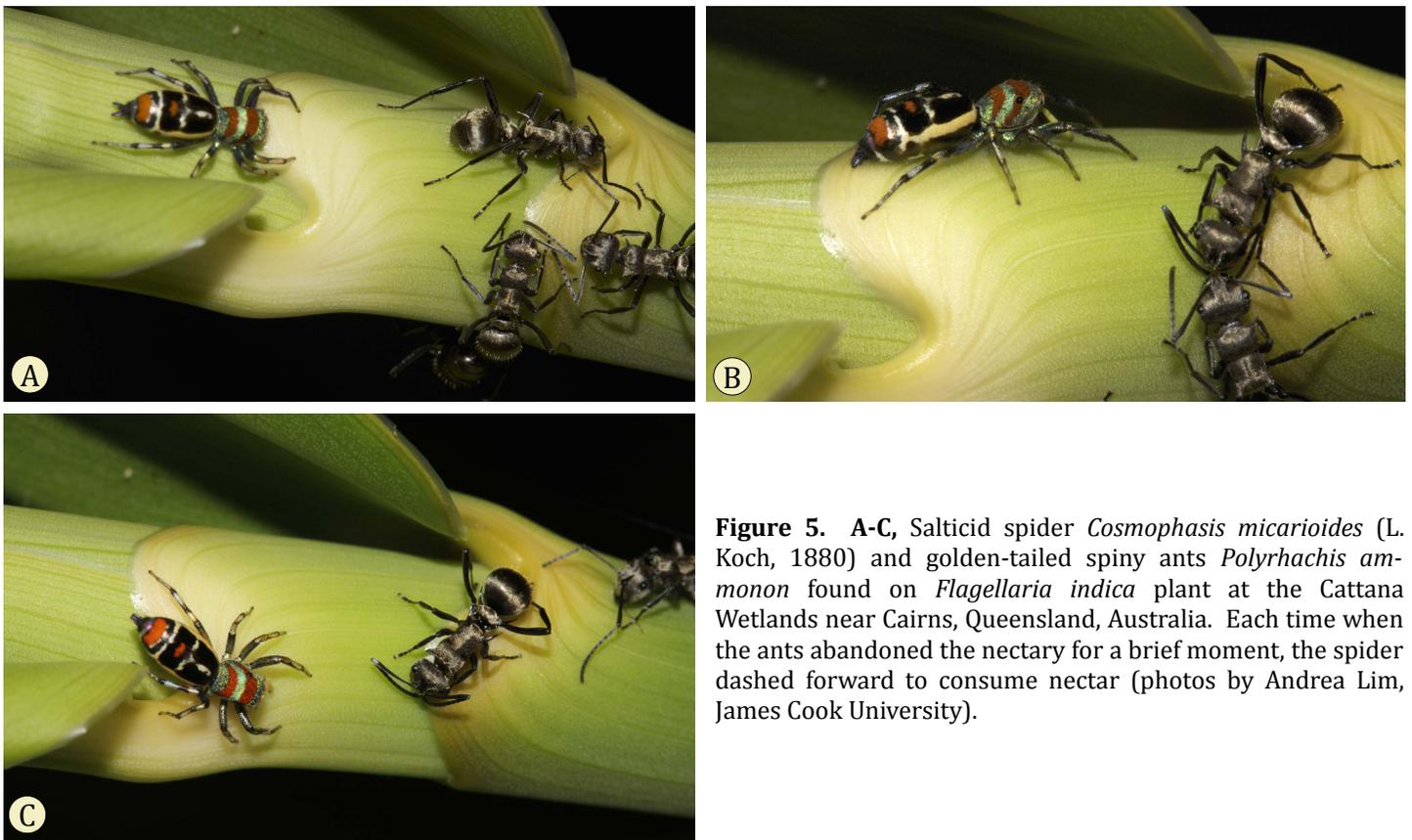
**Figure 2.** Salticid spider *Pelegrina galathea* feeding at extrafloral nectaries of an unspecified shrub (photos taken indoors by David E. Hill, Simpsonville, South Carolina). **A-B**, A sequence of two images of an adult male spider. Note the droplet of nectar in image A. **C-D**, A sequence of two images of an adult female spider. Scale bar = 1.0 mm.



**Figure 3.** A-B, Male *Hentzia mitrata* (Hentz, 1846) at *Prunus* nectary. C, Female *Tutelina elegans* (Hentz, 1846) at nectary of *Prunus*. D-E, Sequence showing a male *Peckhamia* sp. at two nectaries on the same leaf. F, Female *Peckhamia* sp. at nectary. G-H, Immature *Phidippus putnami* (Peckham & Peckham, 1883) at nectary after emerging from brood sac. I, Male *Sassacus papenhoei* Peckham & Peckham, 1895 at nectary. J, Female *S. papenhoei* at nectary. K-L, Female *Maevia inclemens* (Walckenaer, 1837) at nectary. All photos taken indoors by David E. Hill, Simpsonville, South Carolina. Each scale bar = 1.0 mm.



**Figure 4.** **A**, Male salticid spider (*Sassacus papenhoei* Peckham & Peckham, 1895) watching an ant at a nectary. **B**, Female *Tutelina elegans* (Hentz, 1846), an ant predator, watching an ant at nectary. In both examples (A, B) the spider did not attack the ant but at some point later the spider imbibed nectar at one of the nectaries, too, after the ant had left (photos taken indoors by David E. Hill, Simpsonville, South Carolina). Each scale bar = 1.0 mm.



**Figure 5.** **A-C**, Salticid spider *Cosmophasis micarioides* (L. Koch, 1880) and golden-tailed spiny ants *Polyrhachis ammon* found on *Flagellaria indica* plant at the Cattana Wetlands near Cairns, Queensland, Australia. Each time when the ants abandoned the nectary for a brief moment, the spider dashed forward to consume nectar (photos by Andrea Lim, James Cook University).

Another plant-derived product occasionally used as supplementary food by predaceous arthropods is honeydew (Wäckers *et al.* 2008; Lundgren 2009). Honeydew feeding in salticids was reported from Central and East Africa, where ant-mimicking spiders in the genus *Myrmarachne* were seen imbibing honeydew excreted by coccids (scale insects) (Collart 1929; Jackson *et al.* 2008b). Honeydew is surplus sugar excreted in copious amounts by the phloem-feeding coccids (Way 1963). While honeydew constitutes a waste product for the coccids, this sugary liquid otherwise is a food source of high caloric value for ants of the genus *Crematogaster* (Myrmicinae) (Campbell 1994). The ants 'milk' the coccids for their honeydew and at the same time protect them against predators. *Myrmarachne* spiders, which live in close association with these ants (thereby imitating the ants in many aspects of their behavior), have been observed to milk the coccids for their honeydew exactly the way the ants do (Jackson *et al.* 2008b). Jackson *et al.* (2008b) states "...Perhaps feeding on honeydew is disproportionately common in salticids that mimic ants, as honeydew-producing insects tend to attract ants and ants tend to deter most other salticids..." So far only two species of ant-mimicking salticids (*i.e.*, *Myrmarachne foenisex* Simon, 1910 and *Myrmarachne melanotarsa* Wesolowska & Salm, 2002) have been documented to feed on honeydew (Collart 1929; Jackson *et al.* 2008b). However, >200 *Myrmarachne* spp. do occur worldwide (Platnick 2014), and it is most likely that consumption of honeydew does occur in still other species from this genus. Taylor (2004) has shown in a laboratory feeding experiment that newly emerged spiderlings of *Cheiracanthium inclusum* (Hentz, 1847) (Eutichuridae) had a significantly higher life expectancy when offered honeydew as food compared to starving spiderlings. The honeydew used in Taylor's study originated from scale insects (Pseudococcida) infesting mulberry plants (family Moraceae) in a greenhouse. The results of this study have been confirmed in a most recent laboratory study by Pfannenstiel (2015).

A third category of plant food available in liquid form is plant sap, whereby predatory arthropods must pierce leaves with their mandibles or chelicerae in order to get access to this type of food. Piercing leaves by salticids was incidentally witnessed when David Hill took pictures in a film studio in South Carolina (Figure 6). On this occasion, adults of *Pelegrina galathea* (Walckenaer, 1837), *Hentzia mitrata* (Hentz, 1846), and *Maevia inclemens* (Walckenaer, 1837) were seen biting with their chelicerae into leaves of *Rubus* sp. or *Prunus* sp., as it seems, to gain access to plant sap (Figure 6; Hill 2009; David Hill, pers. comm.). Each time after leaves had been pierced, plant sap exuded from the bite holes and the spiders were observed imbibing the exudates with pumping movements after lowering their mouth to the leaf surface (Figure 6; Hill 2011a; David Hill, pers. comm.). Piercing of leaves to extract plant sap has also been observed in other predaceous arthropod taxa, in particular in predatory bugs whose foraging patterns resemble somewhat those of the salticids (*e.g.*, Armer *et al.* 1998). Like salticids the predatory bugs are plant-dwelling, highly mobile predators which forage during the daylight hours (Ruberson *et al.* 1986). Predatory bugs that pierce plants with their stylets have been proven to ingest significant amounts of xylem sap made up largely of water and in addition to this small amounts of mesophyll content (composed of starches, sugars and amino acids) (Armer *et al.* 1998). In contrast to this, it is currently unknown whether salticids ingest phloem, xylem or mesophyll contents when drinking sap from *Rubus* and *Prunus* plants (comp. Armer *et al.* 1998).



**Figure 6.** Salticid spiders feeding on plant sap (all photos taken indoors by David Hill, Simpsonville, South Carolina). **A**, Female *Pelegrina galathea* apparently biting into *Rubus* leaf; note liquid released at leaf surface. **B**, Male *Hentzia mitrata* apparently biting into a *Prunus* leaf; note liquid exuding from the leaf. **C**, Female *Hentzia mitrata* apparently biting a *Prunus* leaf. The exuding liquid associated with this behavior can be seen clearly. **D**, Immature *Phidippus audax* apparently feeding on droplets of solid, crystalline exudate on the surface of a leaf. This exudate may have been the result of leaf damage caused by insects with piercing-sucking mouthparts.

### Feeding on solid plant tissue

A small salticid species that uses solid plant tissue as its principal diet has been discovered during the last decade (Meehan *et al.* 2009; Scully 2012). This unique case of a ‘vegetarian spider’ was documented by researchers from Villanova University and Brandeis University in southeastern Mexico and northwestern Costa Rica, respectively (see Meehan *et al.* 2009). In this particular case, the salticid spider *Bagheera kiplingi* Peckham & Peckham, 1896 had been observed to feed on small, nutritious food bodies – termed as ‘Beltian bodies’ – growing on the leaflet tips of *Vachellia acacias* (Figure 7A). Beltian bodies are produced by the acacias as a food reward for acacia ants (*Pseudomyrmex* spp.) which in return defend the acacias against herbivorous insects (‘ant-acacia mutualism’; Figure 7B). According to Turlings & Wäckers (2004) plant food of this type “can serve as an alternative to insect protein.” Apart from Beltian bodies, *Bagheera kiplingi* has been observed feeding on nectar and tiny insect prey. The silk nests of *Bagheera kiplingi* are found on older acacia branches with less ant traffic (*i.e.*, ‘low ant density nest sites’ sensu Scully [2012]).



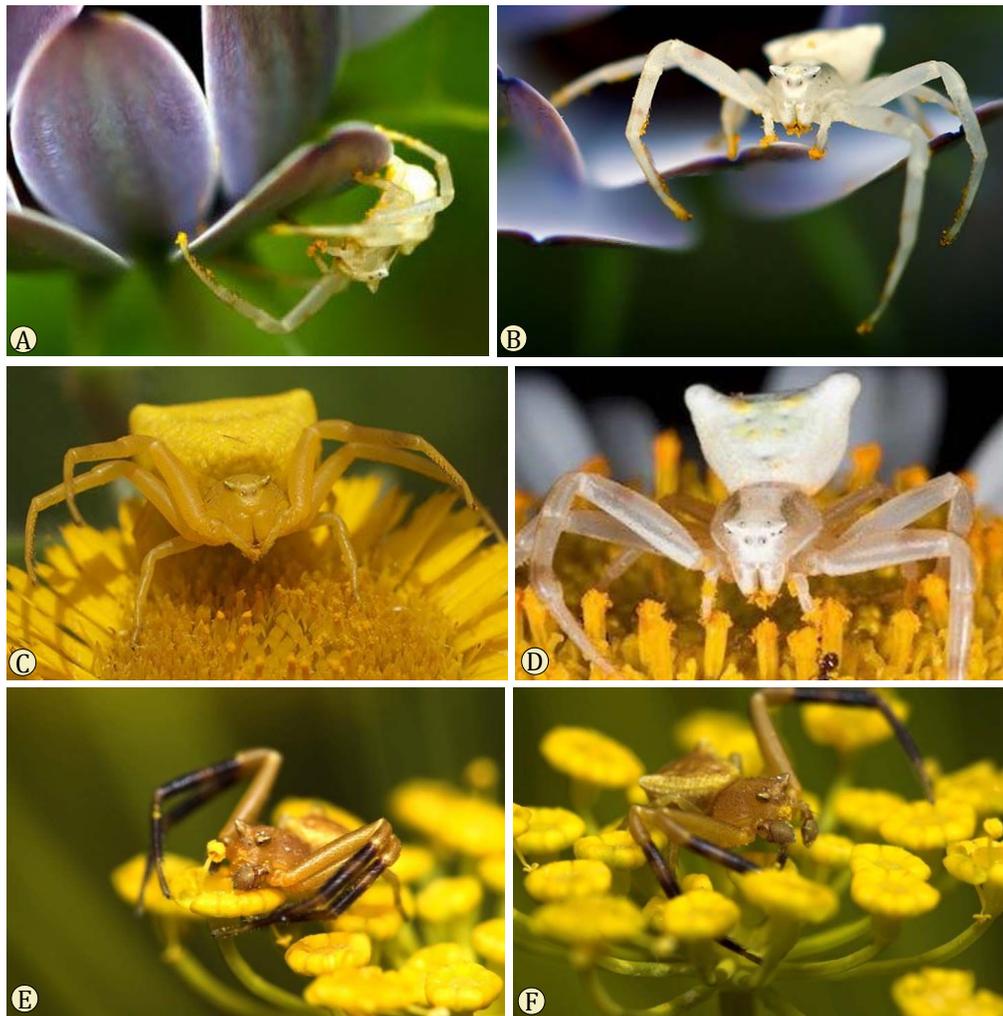
**Figure 7.** **A,** *Bagheera kiplingi* female consuming Beltian body on a *Vachellia collinsii* plant in Akumal, Mexico (Image credit: Robert L. Curry, Villanova University). **B,** *Pseudomyrmex* sp. ant carrying a Beltian body on *Vachellia hindsii* plant near Puerto Escondido, state of Oaxaca, Mexico (Image credit: Martin Heil, Centro de Investigación y de Estudios Avanzados, Mexico).

Hundreds of incidents of consumption of Beltian bodies witnessed at various locations in Mexico indicate that this type of feeding behavior by *Bagheera kiplingi* is routine (Meehan 2009). Plant-derived food (Beltian bodies and nectar) made up >90% of the total diet of *Bagheera kiplingi* in Mexico. During the winter months, when the availability of Beltian bodies decreases, a considerable increase in the level of cannibalism among these spiders was noted in the Mexican study, providing further evidence of the strong dependence of this spider on Beltian bodies as a staple diet (Meehan 2009). Cannibalism in spiders is considered to be a survival strategy during times of low food availability (Wise 2006). In Costa Rica, on the other hand, the proportion of plant material was not as high (~60% of the total diet; Meehan *et al.* 2009). The lower dependence on plant food in the southern part of the geographic range of this spider cannot yet be explained.

A second case of a salticid spider feeding on solid plant material was reported from Kenya. There Nelson & Jackson (2011) took a photo of *Evarcha culicivora* Wesolowska & Jackson, 2003 feeding on pollen of a *Hibiscus* flower. A similar incident of pollinivory in a salticid spider was witnessed by Simon Pollard in a film studio in Bristol, as he was advising on a documentary with the BBC. In this latter incident an unspecified Asian salticid spider was filmed in the process of sucking out the contents of a large pollen grain originating from a bird-pollinated plant (Simon Pollard, pers. comm.). Pollard stated: "...The spider held the pollen grain close to its mouth opening and one could see the grain change colour as the grain was bathed in digestive fluid and the contents were sucked out..." While incidents of pollinivory in free-living salticids seem to be scarce, this type of feeding behavior has more often been noticed in flower-dwelling thomisine spiders (Pollard *et al.* 1995). In a field study in Virginia, Simon Pollard (pers. comm.) was able to witness about a dozen incidents of thomisids consuming pollen grains. Both salticids and thomisids get access to pollen while wandering over flowers (Figures 8-9). Pollen, rich in protein, is utilized as a supplementary food by a broad spectrum of predaceous arthropods including flower bugs (Anthocoridae), green lacewings (Chrysopidae), ground beetles (Carabidae), hoverflies (Syrphidae), ladybugs (Coccinellidae), mantids (Mantidae), and predatory mites (Phytoseiidae) (Lundgren 2009).



**Figure 8.** Salticid (female *Plexippus* sp.) covered with yellow *Hibiscus* pollen in an urban home garden in Kinshasa, Congo (Photo credit: Nick Hobgood, University of South Pacific, Suva, Fiji). It is known from other studies that some African salticids feed on *Hibiscus* pollen (Nelson & Jackson 2011).



**Figure 9.** Flower-dwelling thomisid spiders (Thomisidae) often hold packages of pollen in their chelicerae, and it has been shown in field and laboratory studies that these spiders actually extract nutrients from the pollen (Vogelei & Greissl, 1889; Pollard *et al.*, 1995; Pollard, pers. comm.). **A-B**, *Thomisus* sp. on an asterid flower in Porto Vecchio, Corsica (Image credit: Jean François Bonachera, Porto Vecchio). **C**, Female *Thomisus* sp. on a flower of the family Asteraceae (photo by Alex Miranda, Spain). **D**, Female *Thomisus* sp. on the inflorescence of a flower (aster family) in a park in Bodrum, Turkey (Image credit: Ludmila Yilmaz, Istanbul). **E-F**, Adult male *Thomisus* sp. on an inflorescence of *Ridolfia segetum* (Apiaceae) in a park between Tel Aviv and Jerusalem, Israel (Image credit: Omri Alon, Eilat).

Still another possible way of acquiring solid plant material as potential food was reported by Salm (2005). This author witnessed how salticids in the genus *Menemerus* were snatching plant particles from the mandibles of *Crematogaster* ants; however, it is so far unknown whether the stolen plant particles are digested by the spiders (also see Jackson *et al.* 2008a). This behavior resembles somewhat that of *Bagheera kiplingi* individuals snatching ant larvae from the mandibles of *Pseudomyrmex* worker ants as the ants are transferring brood between thorns of acacias (see Meehan 2009).

## Discussion

Phytophagy in salticid spiders has been documented from all continents of the globe except Antarctica and Europe. The absence of reports from Antarctica is obvious, taking into account that such thermophile spiders do not exist in the cold Antarctic climate (Penney 2008). In contrast, Europe is inhabited by a fair number of salticid species (> 100 species; Proszynski 1978). Why then are there no published reports on phytophagy in European salticids? As Nyffeler *et al.* (2016) pointed out, phytophagy in this spider family is widespread in the warmer areas within the latitudinal band from 40°N to 40°S. This is true in particular in the case of nectar feeding which is most common in subtropical-tropical regions where plants secreting copious nectar are very abundant (Pemberton 1998; Chamberlain & Holland 2009) and where salticids have their main area of distribution (Gertsch 1979; Jackson *et al.* 2008a). The most northern occurrence of nectar consumption by salticids was reported from an area in Michigan (located at 42.7875° N, 86.1089° W; Douglas 1983). Since only a small portion of Europe is located at latitudes below 40° north with warm enough climates, phytophagy in European salticid spiders might be rare compared to other continents. Nonetheless, nectarivory in salticids might occur in some of the southernmost parts of Europe in places where these spiders inhabit plants with copious nectar production (e.g., *Hibiscus*, castor bean, cotton). Organic cotton fields in Andalusia/Spain, for instance, are inhabited by salticids (Pérez-Guerrero *et al.* 2009) and in such environments nectarivory may occur and might be detected by testing field-collected spiders for fructose (a sugar contained in nectars) using cold-anthrone tests (see Taylor & Pfannenstiel 2008).

Plants from many taxa are chemically protected to avoid overexploitation by herbivores (Janzen *et al.* 1977; Lundgren 2009). It should be noted that nectars from >20 plant families contain secondary compounds (i.e., alkaloids, cardenolides, glycosides, and saponins) reported to sometimes cause behavioral changes in arthropods when ingested by them (Stephenson 1981; Adler 2000; Lundgren 2009). For instance, ants that fed on nectar containing iridoid glycosides often became disoriented and as a consequence of this, 27% of the intoxicated ants fell from plants (Stephenson 1981). In another study it was demonstrated that the alkaloid caffeine contained in the nectars of certain flowers significantly altered the foraging behavior of honeybees (Couvillon *et al.* 2014). This begs the question whether ingestion of nectar containing alkaloids, cardenolides etc. might alter the behavior of salticids as well. To date, studies on the effects of alkaloids, cardenolides etc. on free-living spiders are lacking, but scientists have at the very least a few indications of this based on laboratory studies conducted on non-salticid spiders. During the last 60 years, extensive studies on the effects of behavior-altering drugs on spider central nervous systems were conducted (i.e., using orb-weaving spiders as model systems) and, as chance would have it, several of the tested substances were plant-based alkaloids (Witt 1956; Witt 1971; Noever *et al.* 1995; Hesselberg & Vollrath 2004). When plant-based alkaloids such as atropine, caffeine, mescaline, pilocarpine, physostigmine, scopolamine and strychnine were offered to spiders dissolved in a solution of sugar water, the spiders quickly imbibed these substances, and this was followed by significant behavioral changes (see Wolff & Hempel 1951; Witt 1956; Christiansen *et al.* 1962; Witt & Reed 1965; Noever *et al.* 1995). In particular, size and shape of orb-webs were severely altered after ingestion of these alkaloids.

Though defensive chemicals such as alkaloids or glycosides are distasteful (see Brown 1984; Masters 1990; Eisner & Eisner 1991; Kumar *et al.* 2014), their distastefulness might be less recognizable when dissolved in a sugary solution (bitter taste being 'masked' by the sweet flavor of sugars). While some substances were fed to the spiders in fairly high doses (*e.g.*, caffeine and mescaline at a dose of  $\sim 0.1$  mg per spider), others have proven to be effective even at a very low dose (*e.g.*, atropine and physostigmine at a dose of  $\sim 0.0001$  mg per spider) (Witt & Reed 1965). Similar behavior-altering effects were obtained when spiders were fed plant-based cardenolides or fungal alkaloids (Christiansen *et al.* 1962; Witt & Reed 1965; Malcolm 1989). These experiments suggest that alkaloids and cardenolides, when ingested by the spiders, may drastically affect their nervous systems. Admittedly these experiments have been conducted with non-salticid spiders and in captivity (the test substances being delivered in sugar water as a nectar surrogate). Notwithstanding, it seems highly likely that free-living salticids occasionally imbibe floral nectar that contains alkaloids or other defensive chemicals (*e.g.*, nectar from *Ixora javanica* flowers; Lim & Li 2004) and if salticid nervous systems react in a similar way to such chemicals as the 'test spiders' in above mentioned experiments did (Witt & Reed 1965), then it can be assumed that salticids imbibing nectar from flowers might sometimes result in behavioral changes in the real world as well. But again, the fact that floral nectar is apparently consumed much less frequently than extrafloral nectar (extrafloral nectar usually does not contain any defensive chemicals) suggests that ingestion of alkaloids, cardenolides etc. might be an issue of secondary importance to salticids. Much still remains to be explored in this area of research.

It might be added that Hill (2006) presented a study in which the jumping spider *Phidippus audax* was unable to detect the cardenolides Ouabain and Digitoxin offered to this spider in the form of prey flies that had been treated with these chemicals. Hill states "Spiders readily fed on a toxic dose of these cardenolides, and many of the spiders were immobilized and later died, presumably as a result of this experience."

Digestive enzymes, which originate in the gut and are released from the spiders' oral cavity, are key during feeding on plant material (Cohen 1995). Generally speaking, spiders are fluid feeders that can ingest food particles (up to  $\sim 1 \mu\text{m}$   $\emptyset$ ) exclusively as a semi-liquid soup (Foelix 2011; Hill 2011b). Considering that plant foods occur in liquid or solid state, there are basically two main ways that plant foods are digested by spiders. Firstly, plant materials available in a liquid state such as nectar, honeydew or plant sap can be sucked in through the mouth opening without any difficulties (Jackson *et al.* 2001). Sucrose contained in these sugary products is thought to be broken down into its monosaccharide components by means of the enzymes sucrase and  $\alpha$ -glucosidases present in the digestive juices of spiders (Pickford 1942; Mommsen 1978a; Taylor 2004). Secondly, plant material which is available in a solid state such as Beltian bodies or pollen has to be first transformed into a liquid state by means of extraintestinal digestion before it can be imbibed. Spiders are equipped with all enzymes needed to digest solid plant material with the exception of exinase (Pickford 1942; Mommsen 1978a, 1978b, 1978c, 1978d; Collatz 1987; Taylor 2004). Exinase, however, is needed to enzymatically break down the exine, a starchy protective shell that covers the nutritious content of pollen grains (Vogelei & Greissl 1989; Johnson & Nicolson 2001; Pfannenstiel 2012). How then are spiders capable of digesting pollen? Smith & Mommsen (1984) assumed that nutrients are probably extracted from the pollen grains through tiny apertures in the pollen wall. Other authors noticed that the pollen mass held between the spiders' chelicerae was mechanically processed through alternative cheliceral movements, often in concert with other mouthparts, breaking, crushing or at least rupturing the exine and thereby releasing the nutritious pollen content which is then bathed in a bubble of digestive juice released from the spider's oral cavity (Flechtmann & McMurtry 1992; Peterson *et al.* 2010; Pfannenstiel 2012; Simon Pollard, pers. comm.). In the course of this process, the pollen mass turns into a soupy mixture made up of dissolved pollen tissue and digestive juice, which is imbibed after a while through the spider's mouth opening (Hill 2011b). The

ability of certain spiders to feed on Beltian bodies might be explained by the presence of proteases of the chymotrypsin-type (not inhibited by plant-derived Kunitz-type protease inhibitors) in their digestive tracts (Orona-Tamago *et al.* 2013). To sum up, it can be said that it seems to be well understood how spiders accomplish the digestion of liquid plant food, whereas the ability to digest solid plant tissue is still not fully understood.

Regarding the digestive processes that spiders have to accomplish, the following might be added (David Hill, pers. comm.): “One thing that strikes me is that the insects that spiders feed on must have, in addition to some sequestered compounds, quite a bit of undigested material in their gut, as well as a lot of symbionts that produce their own products of digestion. Spiders must be able to deal with all of this. I think of an aphid loaded with plant nectar, a fly filled with tree sap, or a caterpillar filled with chewed leaves.” This point has also been briefly discussed in Nyffeler *et al.* (2016).

Nectarivory has been reported for still another spider group, namely the ‘nocturnal runners’ (Taylor & Foster 1996; Taylor & Pfannenstiel 2008, 2009; Taylor & Bradley 2009; Suetsugu *et al.* 2014). This spider group – belonging to the Dionycha clade like the salticids – is made up of the families Anyphaenidae, Clubionidae, Eutichuridae, and Trachelidae (see Taylor 2004). Nocturnal runners are sometimes found on the same host plant species (*e.g.*, castor bean *Ricinus communis* L.) as salticids and like the salticids they move over the plants in search of food, stopping from time to time at nectaries to imbibe nectar (Figure 10; Taylor & Foster 1996; Patt & Pfannenstiel 2008, 2009). In Figure 11 a nocturnal runner of the genus *Cheiracanthium* (family Eutichuridae) is depicted drinking from a drop of sugar water. The extent to which the nocturnal runners make use of nectar as a source of nutrients is still largely unexplored which might be explained by the fact that such nocturnal foragers are active at a time of the day when most arachnologists are asleep (also see Eberhard *et al.* 1978; Taylor & Foster 1996).



**Figure 10.** Nocturnal runners (Anyphaenidae) consuming nectar (photos by Woodbridge Foster, Ohio State University). **A**, *Hibana velox* (Becker, 1879) feeding at paired extrafloral nectaries at the base of a leaf of the castor bean *Ricinus communis* in Vero Beach, Florida. **B**, *Hibana similaris* (Banks, 1929) pressing mouthparts to nectar-bearing trichomes at panicle branch of cashew tree *Anacardium occidentale* on Majé Island, Panama.



**Figure 11.** Nocturnal running spider *Cheiracanthium* sp. (Eutichuridae) drinking from a drop of sugar water in the laboratory (photo by Robin Taylor, Ohio State University). Spiders from this genus are known to feed on nectar and pollen (see Taylor & Foster 1996; Pfannenstiel 2012).

The fact that the only confirmed example of a specialized plant feeder among spiders (*i.e.*, *Bagheera kiplingi*) is a salticid is noteworthy, since although salticids by and large are generalists with broad diets compared to other spiders (*e.g.*, Nyffeler 1999; Ross 2008), this family does at the same time contain a number of species characterized as dietary specialists, usually specializing on ants, termites or spiders as prey (*e.g.*, Edwards *et al.* 1974; Jackson & Hallas 1990; Wesolowska & Haddad 2002). Time will tell whether still other examples of specialized plant-eating spider species will be found somewhere on this globe. In that regard it might be noteworthy that Vollrath (1978) hypothesized about 40 years ago that some species in the spider family Symphytognathidae might be “vegetarians.” The symphytognathids are a tropical family composed of tiny spiders  $\leq 1$  mm in length (Forster & Platnick 1977; Coddington 2005). Vollrath’s speculation was based on the observation that symphytognathids have a very peculiar mouthpart morphology typical of arthropods with a specialized vegetarian lifestyle (compare Forster & Platnick 1977; Labandeira 1997). Tiny, fine-meshed orb-webs (suitable for sieving the aerial plankton for spores or pollen) coupled with the observation that symphytognathids consistently refused to eat any type of small insect prey offered to them under laboratory conditions, might be further evidence of a vegetarian diet of these spiders (Vollrath 1978). Coddington (2005) noted that the speculation that these spiders might be specialized vegetarians would be quite plausible although this has not been substantiated so far.

The significance of phytophagy for spider nutrition is currently still a matter of controversy. Beyond the family Salticidae, several studies demonstrated that supplementary feeding on plant foods had a positive effect on spider fitness (*e.g.*, Smith & Mommsen 1984; Vogelei & Greissl 1989; Pollard *et al.* 1995; Taylor & Bradley 2009). Some authors suggested that the sugar contained in sugary fluids (*i.e.*, nectar and honeydew) might be used as fuel to maintain the elevated energy expenditure associated with the salticids’ high mobility (Jackson & Pollard 1996; Jackson *et al.* 2001; Koptur 2005). Notwithstanding this, other scientists consider plant-eating by spiders in general as more of a marginal phenomenon (Pekár & Toft 2015). Ruberson *et al.* (1986) sums up the importance of plant foods for predators as follows: “The ability of a predator to derive nutrients from plant material may be an adaptation that allows exploitation of a readily available resource during periods when prey are scarce.” This statement referring to arthropod predators in general might apply to salticid spiders as well. Furthermore, enriching the spiders’ diets with plant materials leads to a more diverse diet, a process considered to be advantageous from a nutritional point of view, since diet mixing is optimising a balanced intake of essential nutrients (compare Greenstone 1979; Uetz *et al.* 1992; Toft 1999; Oelbermann & Scheu 2002; Nyffeler *et al.* 2016).

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