

REVIEW

Plant-eating by spiders

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Abstract. Spiders, a group of predominantly insectivorous predators, occasionally use plant food to supplement their insect prey. In the current review, we tracked down 95 reported incidents of spiders feeding on plant food under natural conditions. Globally, >60 spider species representing ten families have been observed feeding on plant materials from over 20 plant families. Cursorial spiders including the families Anyphaenidae, Clubionidae, Eutichuridae, Salticidae, Thomisidae, and Trachelidae dominate among the spiders feeding on plant food (>80% of reported incidents). Spiders feed on a wide diversity of plant-derived products including floral nectar, extrafloral nectar, stigmatic exudate, plant sap, honeydew, seeds, Beltian bodies, Müllerian bodies and pollen (originating from very different plant types such as coniferous and deciduous trees, herbaceous plants and shrubs, annual weeds, grasses, climbing plants, orchids, carnivorous plants, and ferns). Furthermore, spiders have been shown to consume fungal spores in laboratory trials. Supplementary feeding on plant materials by spiders was shown to be global in extent and widespread across spider taxa, plant taxa and plant materials; however, the extent to which the different categories of plant food contribute to the spiders’ diet and how this may affect their behavior and life history is still largely unexplored. This review is expected to lay a foundation for future research on this topic.

Keywords: Food bodies, honeydew, nectar, nutritional ecology, plant-derived food, pollen

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1. INTRODUCTION

Spiders are a speciose arthropod group with a wide variety of ecological niches, yet they have been conventionally described as

predators feeding almost exclusively on live insects (Whitcomb 1974; Sunderland et al. 1986; Young & Edwards 1990). More recent studies broadened our understanding of spider foraging

behaviors and diet composition, including observations of spiders feeding on prey such as crustaceans, earthworms, gastropods, and a variety of small vertebrates (Symondson et al. 2002; Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014). There is also a growing set of reports of spiders feeding on static foods such as arthropod eggs and dead insects (Pfannenstiel 2008; Vetter 2011; Peng et al. 2013; Vickers et al. 2014). Captive spiders have fed on unusual foods such as sausage, banana, grapes (Decae 1986; Schultz & Schultz 2009) and soy milk (Amalin et al. 1999, 2001), and have been successfully raised on artificial diets composed of milk and egg yolk mixtures (Peck & Whitcomb 1968; Amalin et al. 1999, 2001). Spiders readily imbibe sugar water (Witt 1971; Lanza 1988), and have been observed visiting hummingbird feeders (Stoaks 2009).

Reports of spiders feeding on plant products in nature first appeared in recent decades. Smith & Mommsen (1984) reported that the webs of immature cribellate orb-weavers are pollen collectors and that the pollen grains adhering to the sticky threads are unintentionally ingested along with the old silk material when the spiderlings are recycling their webs. Pollard et al. (1995) as well as Taylor & Foster (1996) documented cases of spider nectarivory from North America and Central America. Since those early reports, there have been many more discoveries of spiders feeding on plant materials (e.g., Vogeley & Greissl 1989; Ruhren & Handel 1999; Jackson et al. 2001; Blüthgen & Reifensath 2003) including a remarkable case of a salticid, *Bagheera kiplingi* Peckham & Peckham, 1896, that derives the majority of its nutrition from plant resources (Meehan et al. 2009). So far information on plant-eating spiders has been widely scattered throughout the literature and a comprehensive review covering this topic was missing. To close this gap, a systematic review on plant-eating spiders was conducted and the insights from this research are presented here.

2. METHODS

An extensive bibliographic search was carried out to locate reports on spiders feeding on plant materials. The search was based largely on the Thomson-Reuters database, Web of Science (all data bases), Google Scholar, Google Books, and ProQuest Dissertations & Theses. In addition to this, an internet search for information on this topic was conducted, and authors of internet reports on spider phytophagy were contacted to obtain additional information on their observations. Furthermore, biology books and journals not included in the large data bases were hand-searched and arachnologists and field biologists with known interest in spider phytophagy were contacted to request unpublished reports on this topic. Reports of feeding on fungi as a type of vegetarian food (in contrast to food of animal origin) were included despite the fact that fungi, taxonomically, do not belong to the plant kingdom.

With the exception of two records relating to orb-weavers assessed by stable isotope analyses (see Eggs & Sanders 2013), the core data used in this paper are based on direct observation in the field (see Appendix 1). The problem with laboratory feeding studies is that they are in many cases not reliable. For instance, spiders have been considered to be nectarivorous based on the observation that they drink sucrose solutions in laboratory tests (e.g., Vogeley & Greissl 1989; Pollard et al. 1995; Jackson et al. 2001; Milne 2010; Wu et al. 2011; Pfannenstiel & Patt 2012). However, according to Lundgren (2009), a wide variety

of predaceous arthropods tested in the lab all accepted sucrose solutions, thus such studies cannot be considered to be conclusive evidence for nectarivory. Other researchers reported that spiders are nectarivorous because of positive cold anthrone test results (Taylor & Pfannenstiel 2008; Chen et al. 2010), but these wild-caught spiders may have acquired a high sugar content indirectly by preying on well-fed nectarivorous insects (Wilder 2011). Despite all these concerns, experimental laboratory studies provide valuable supportive evidence for the field observational studies reviewed in this paper (Appendix 1) and therefore are included in the discussion.

A total of 95 records of plant-feeding by spiders was gathered (Appendix 1). Eighty-two (86%) of these were previously reported in the scientific literature and roughly 20% included photographic documentation of phytophagy. Nomenclature of spiders follows Platnick (2014).

3. RESULTS

Feeding on plant food by spiders is global in extent, as such behavior has been reported from all continents except Antarctica. Spiders have been observed to feed on a wide variety of different types of plant products, with floral nectar and extrafloral nectar dominating (~75% of all reported incidents). We classified the reported incidents of plant feeding into five major groups: 1. Leaf feeders, 2. Sugar feeders, 3. Pollen feeders, 4. Seed feeders, and 5. Spore feeders (see Lundgren 2009). In addition to this, we briefly mention the possibility that plant food in the guts of herbivores eaten by spiders will be ingested unintentionally along with the dissolved prey tissue.

3.1 Spiders as leaf feeders.—Spiders cannot ingest solid particles, so by ‘leaf feeders’ we mean both a) instances of spiders biting off or otherwise removing pieces of leaves and extra-orally enzymatically dissolving them prior to ingesting, or b) piercing leaves with their chelicerae to extract plant sap. We hereby view feeding on Beltian bodies and Müllerian bodies, respectively, as a special case of leaf-feeding because these small oval-shaped multicellular structures are produced on the leaflet tips or on leaf petioles (Rickson 1976; Meehan 2009).

3.1.1 Feeding on Beltian bodies: A major case of a leaf feeder is that of *Bagheera kiplingi*, a salticid spider reported to depend largely on plant food (Fig. 1A, B; Jackson 2009; Meehan et al. 2009). *Bagheera kiplingi* has been collected from southeastern Mexico to northwestern Costa Rica, coincident with the range of the Central American ant acacias (*Vachellia* spp., Fabaceae) on which it is apparently an obligate resident (Meehan et al. 2009; Scully 2012; Eric Olson, pers. obs.). The well-studied ant-plant mutualism leads to the production of extrafloral nectar and peculiar lipid and protein-rich food bodies of high nutritional value (i.e., ‘Beltian bodies’) harvested by *Pseudomyrmex* spp. ants (Pseudomyrmecinae), which in return patrol the foliage and stems acting as ‘plant bodyguards’. The spider *B. kiplingi* (5–6 mm adult body length) exploits this mutualism in several ways, but most strikingly by harvesting Beltian bodies (Fig. 1A). *Bagheera kiplingi* individuals of all ages from neonates to adults, and of both sexes, pluck Beltian bodies from leaflet tips. An adult or large subadult spider can consume a single food body in less than four minutes and on one occasion an adult female consumed 36 Beltian bodies in a single feeding episode, representing 10% of the food bodies on one acacia leaf (Eric Olson, pers. obs.). That particular spider specimen had

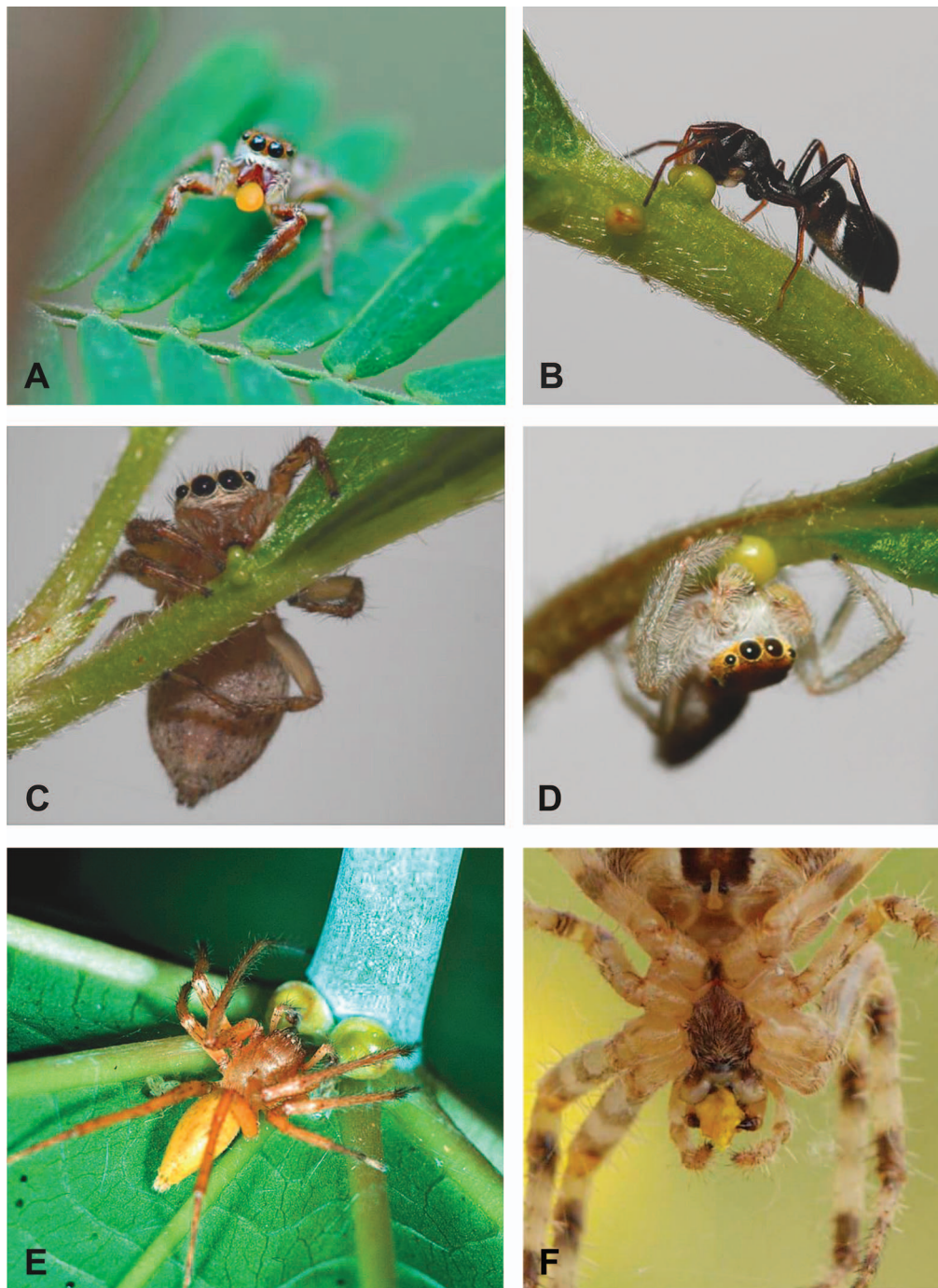


Figure 1.—Plant-eating by spiders. A. Juvenile *Bagheera kiplingi* consuming a Beltian body on a *Vachellia collinsii* plant in Akumal, Mexico (photo by E. J. Scully); B. Adult female salticid spider *Peckhamia* sp. drinking nectar at an extrafloral nectary of *Prunus* sp. (photo by D. E. Hill); C. Adult female *Maevia inclemens* (Walckenaer, 1837) feeding at extrafloral nectaries of *Prunus* sp. (photo by D. E. Hill); D. Male *Hentzia mitrata* imbibing nectar from an extrafloral nectary of a *Prunus* shrub (photo by D. E. Hill); E. *Hibana velox* feeding at paired extrafloral nectaries of a castor bean plant in Vero Beach, FL (photo by W. A. Foster); F. Adult female *Araneus diadematus* digesting a pollen package left behind by an escaping wild bee on the edge of a field near Munich, Germany (photo by C. Ludy).

been kept in the laboratory for several days without food and was then released onto a plant with a weak ant colony, where it was able to feed with impunity (Eric Olson, pers. obs.). At first glance it may appear that this is quite a large quantity of food. However, the weight of a single Beltian body ≤ 1 mm in length is very low (~ 0.5 mg fresh weight / food body) and harvesting three dozen Beltian bodies results in an amount of food of only ~ 18 mg fresh weight which is the equivalent of one small insect prey.

In addition to Beltian bodies, *B. kiplingi* regularly take nectar from their host plants' abundant extrafloral nectaries,

consume ant larvae, which the spiders seize from worker ants as the ants are transferring brood between thorns, and occasionally kill minute dipterans and other insect prey. Insect prey is scarce on vigorously defended ant-acacias, and plant-derived food made up $>90\%$ of the recorded foraging events at the Mexico location. In Costa Rica, the proportion of plant material was lower ($\sim 60\%$) and that of insect prey (*Pseudomyrmex* larvae and small dipterans) higher ($\sim 40\%$) (Meehan et al. 2009).

During a seven-year salticid inventory in Costa Rica, 48 salticid species were encountered (N = 1,174 individuals) but,

apart from *B. kiplingi*, none of these salticid spiders was witnessed feeding on Beltian bodies, indicating that the use of this type of food by *B. kiplingi* might be unique among salticid spiders (Eric Olson, pers. obs.). This notwithstanding, researchers from Villanova University, USA, are currently investigating whether additional salticid species might be found that feed on Beltian bodies (Eastburn 2014).

3.1.2 Feeding on Müllerian bodies: A second example of consumption of leaf material by spiders has been reported from the Rio de Janeiro area, Brazil, where a nocturnal running spider of the genus *Clubiona* Latreille, 1804 (Clubionidae) was seen feeding on food bodies produced by *Cecropia* trees (Urticaceae) (Andrade 1981; Jolivet 1988). The food bodies on the leaf petioles of *Cecropia* trees (termed 'Müllerian bodies') are small (~0.3 mm x 1.0 mm) and are composed primarily of the carbohydrate glycogen but also contain lipids, proteins, and amino acids (Rickson 1973). *Cecropia* trees are also inhabited by ants in many environments, most commonly *Azteca* spp. (Dolichoderinae), some species of which are obligate *Cecropia* inhabitants that (at least in some settings) defend *Cecropia* trees against some herbivores (e.g., Vasconcelos and Casimiro 1997). Müllerian bodies are harvested by resident *Azteca* ants and are a significant food source for their larvae (Sagers et al. 2000). To date, *Clubiona* spiders have been spotted on only a few occasions consuming Müllerian bodies (Andrade 1981; Jolivet 1988) and the relative importance of these food bodies in spider nutrition remains unknown.

3.1.3 Feeding on plant sap: A third example of spiders as leaf feeders was reported by Stejskal (1976) from a mango plantation (Anacardiaceae) in eastern Venezuela, where immatures and adults of an unspecified species in the genus *Anelosimus* Simon, 1891 (Theridiidae) were observed biting with their chelicerae into mango leaves (also see Fowler & Levi 1979; Agnarsson 2006). The species in question was later identified by Agnarsson (2005) to be *Anelosimus rupununi* Levi, 1956. After piercing the epidermis on the leaves' underside, the spiders were imbibing plant sap (Stejskal 1976). The spiders were also observed preying on insects, as is common behavior in *Anelosimus* spp. (Levi 1972; Fowler & Levi 1979; Vollrath & Rohde-Arndt 1983). Spiders in this genus appear often to be food-limited which might explain the need of *A. rupununi* to supplement its insect diet by additionally imbibing plant sap (see Vollrath & Rohde-Arndt 1983). In this Venezuelan study, *A. rupununi* was found exclusively on mango, citrus, and coffee trees (Stejskal 1976) which fits observations from Trinidad and Surinam (Levi 1972). Fowler & Levi (1979) suggested that Stejskal's studies should be followed up in order to confirm the unusual leaf piercing behavior of these spiders.

A study by Hajer (1988) conducted under laboratory conditions seems to confirm Stejskal's observation that certain spiders occasionally pierce leaves to gain access to plant sap. While using *Philodendron scandens* K. Koch & Sello (family Araceae) as a plant substrate to breed *Nigma flavescens* (Walckenaer, 1830) (Dictynidae), this author witnessed destruction of the leaf surface down to the mesophyll level. Hajer (1988) concluded that "the content of the plant cells had been apparently used by nymphs of 1st instar as a source of food".

Indoor observations by David Hill on three North American salticid spiders provide further evidence for spiders feeding on plant sap. This researcher repeatedly witnessed adults of

Pelegrina galathea (Walckenaer, 1837), *Hentzia mitrata* (Hentz, 1846), and *Maevia inclemens* (Walckenaer, 1837) biting with their chelicerae into leaves of *Rubus* sp. or *Prunus* sp. (Hill 2009; David Hill, pers. comm.). Each time after leaves had been pierced, plant sap exuded from the bite holes. The spiders were seen lowering their mouthparts to the leaf surface, apparently sipping from the liquid with pumping movements (Hill 2011; David Hill, pers. comm.). Furthermore, an immature *Phidippus audax* (Hentz, 1845) was observed feeding on small droplets of crystalline exudate on the upper surface of a leaf under laboratory conditions (David Hill, pers. comm.). Consumption of crystallized materials, such as dried sugar solutions, by predaceous arthropods has been reported previously in the literature (Bartlett 1962; Lundgren 2009).

3.2 Spiders as sugar feeders.—Animals are defined as 'sugar feeders' when they feed on liquids with a high sugar content (Lundgren 2009). This type of feeding encompasses consumption of sugary plant-derived products such as floral nectar, extrafloral nectar, and honeydew. The stigmatic exudate produced by the flowers of Winteraceae trees is included in this category of plant products due to its functional similarity to floral nectar (Richards 1997).

3.2.1 Feeding on floral nectar: Jumping spiders (Salticidae) from >30 different species have been witnessed imbibing nectar from floral nectaries in the wild (Jackson et al. 2001; Lim & Li 2004; Cross & Jackson 2009). Likewise, drinking of floral nectar has been observed in nocturnal running spiders of the families Anyphaenidae, Clubionidae, Eutichuridae, and Trachelidae (Taylor & Foster 1996; Taylor 2004; Suetsugu et al. 2014). Furthermore, there are reports of flower-dwelling thomisid spiders in the subfamily Thomisinae (genera *Misumena*, *Misumenoides*, and *Thomisus*) imbibing nectar from the flowers of a variety of plants (Vogelei & Greissl 1989; Pollard 1993; Pollard et al. 1995; Morse 2007). During such incidents, the spiders were seen pushing their mouthparts deep into flowers to drink nectar, similar to the way nectar-drinking insects feed (Pollard 1993; Taylor & Foster 1996; Jackson et al. 2001; Suetsugu et al. 2014). According to Jackson et al. (2001) the spiders sometimes "positioned their chelicerae around flowers and inserted their fangs". Usually the spiders visit multiple flowers in succession, spending a few seconds up to a few minutes at each flower (Pollard et al. 1995; Taylor & Foster 1996; Suetsugu et al. 2014). In extreme cases, a single spider may visit 60–80 flowers in one hour (Pollard et al. 1995). Quite a number of studies suggest that chemical cues, both olfactory and gustatory, are used to detect and locate nectar sources (Taylor 2004; Patt & Pfannenstiel 2008, 2009; Cross & Jackson 2009). Spiders are attracted to flower fragrances such as eugenol (Krell & Krämer 1998; Dodson et al. 2013).

3.2.2 Feeding on extrafloral nectar: There are reports from many parts of the world of salticid spiders drinking nectar from the extrafloral nectaries of a variety of different plants (Fig. 1B–D; Edmunds 1978; Douglas 1983; Ruhren & Handel 1999; Blüthgen & Reifenrath 2003; Cross & Jackson 2009; Hill 2011; Soren & Chowdhury 2011; Nahas et al. 2012; Hill & Edwards 2013; Mondal et al. 2013). For the ant acacia specialist *B. kiplingi*, that frequently visits nectaries, extrafloral nectar may be more important as a source of moisture than of sugar, at least during dry periods (Eric Olson, pers. obs.).

However, in other spider species, extrafloral nectar has been implicated as an important source of energy that increases their lifespan (Taylor & Foster 1996; Nelson 2004; Taylor & Bradley 2009; Taylor & Pfannenstiel 2009). Drinking of extrafloral nectar has also been witnessed in spiders of the families Anyphaenidae, Eutichuridae, Linyphiidae, Oxyopidae, Thomisidae, and Trachelidae (Fig. 1E; Taylor & Foster 1996; Chen et al. 2010; Nahas et al. 2012; Nico Blüthgen, pers. comm.; Marc Milne, pers. comm.). In many cases, in order to get access to extrafloral nectaries, the spiders have to break through the ant-plant bodyguard defenses (Soren & Chowdhury 2011; Nico Blüthgen, pers. comm.).

That the spiders actually consume nectar has been demonstrated by testing field-collected spiders for fructose (a sugar contained in nectars) using cold-anthrone tests. In such studies it was shown that ~20–30% of all field collected spiders tested positive for fructose, which is indicative for nectarivory (Taylor & Pfannenstiel 2008; Chen et al. 2010).

3.2.3 Feeding on honeydew: Honeydew is a plant-derived sugary fluid excreted by phloem-feeding insects (e.g., coccids and aphids; order Homoptera) after passing through their digestive tracts (Douglas 2006; Lundgren 2009). Consumption of this energy-rich food source has been observed in two species of salticid spiders, *Myrmarachne foenisex* Simon, 1910 and *M. melanotarsa* Wesolowska & Salm, 2002, both of which live in close association with ants of the genus *Crematogaster* (Myrmicinae). Such unusual feeding behavior by *Myrmarachne* spp. has been witnessed in Africa, where the spiders were observed imbibing honeydew while tending scale insects (coccids) alongside ants (Collart 1929; Salm 2005; Jackson et al. 2008).

Furthermore, there are anecdotal reports from Europe of web-building spiders imbibing droplets of honeydew (Bristowe 1941; Kirchner 1964; Stephan Scheurer, pers. comm.). It has been witnessed numerous times that linyphiids and araneids did imbibe droplets of honeydew falling down on their webs from pine trees, *Pinus sylvestris* L. (Stephan Scheurer, pers. comm.). These incidents always occurred in September at a time when the aphids *Schizolachmus pineti* (Fabricius, 1781) and *Cinara pinea* (Mordvilko, 1895) were excreting honeydew while sucking on pine needles. Bristowe (1941) stated that a sheet-web spider (*Linyphia triangularis* (Clerck, 1757)) “...suck drops of honeydew raining down on its web from overhanging trees, but the flavor of this was evidently distasteful because this was always followed by the spider running to the edge of its web to wipe its mouth on a leaf...” Honeydew sometimes contains plant-derived defensive chemicals such as alkaloids or cardenolides, originating from the scale insects’ host plants, which can give it a bitter flavor or even render it toxic (Lundgren 2009). The effects of unpalatable or toxic honeydew on predators are still largely unexplored.

3.2.4 Feeding on stigmatic exudate: A spider of the genus *Thwaitesia* O. Pickard-Cambridge, 1881 (Theridiidae) was seen drinking stigmatic exudate in an open flower of *Drimys granadensis* L.f. (Marquinez et al. 2010). As with floral nectar, the glittering stigmatic exudate of this flower functions to attract insect pollinators (Gottsberger et al. 1980). Stigmatic exudate is rich in lipids and amino acids, but has a low sugar content compared to floral nectar (Frame 2003). Whether the incident reported by Marquinez et al. (2010) was merely

a chance event or a regular occurrence remains to be further investigated.

3.3 Spiders as pollen feeders.—Pollen production can potentially provide spiders with a supplementary food source available in large quantities (Peterson et al. 2010). For example, pollen production amounts to ~100–300 kg fresh weight per ha per year in deciduous forests and to ≤460 kg per ha per year in grassland (Smart et al. 1979; Saito et al. 1991, 2006). Feeding on pollen by spiders can take place in different ways. Firstly, plant-dwelling cursorial spiders encounter pollen grains or pollinia while wandering over flowers (Jennings et al. 1989; Nyoka & Ferguson 1999). In particular, thomisids, salticids, and clubionids have been witnessed consuming pollen grains (Pollard et al. 1995; Nelson & Jackson 2011; Suetsugu et al. 2014). This has also been confirmed for eutichurids under laboratory conditions (Pfannenstiel 2012). Cursorial spiders were reported feeding on pollen from plants of the families Apiaceae, Asteraceae, Malvaceae, and Orchidaceae (Appendix 1). A special case is given when clubionid or thomisid spiders are biting the pollinia off orchid flowers (Suetsugu et al. 2014).

Pollen may also become available to spiders after being transported to the spiders’ webs by pollen-carrying insects (Cook et al. 1981; Beardsell et al. 1986; Craig & Ebert 1994, Ludy 2004). Craig & Ebert (1994) found that a high percentage of pollen-carrying wild bees intercepted in webs of large orb-weaving spiders, were able to escape leaving the pollen they were carrying behind. These authors suggest that the use of left-behind pollen as a concentrated source of nutrients may play a beneficial role in the nutritional ecology of some species of orb-weaving spiders. For example an adult orb-weaving spider, *Araneus diadematus* Clerck, 1757 consumed a package of pollen grains after it was left behind by an escaping wild bee temporarily entangled in the spider’s web (Fig. 1F; Ludy 2004). A similar case was also reported for an adult female orb-weaver, *Gasteracantha cancriformis* (Linnaeus, 1758) (Araneidae) eating pollen from the corbicula of a captured bee’s leg (Gregory 1989).

Pollen transported via air currents can also get trapped in the sticky threads of aerial webs (Smith & Mommsen 1984; Linskens et al. 1993; Del Fiol et al. 2007). Such airborne particles become highly electrostatically charged when moving through the air, which enhances their likelihood of entrapment in spider webs (Ortega-Jimenez & Dudley 2013; Vollrath & Edmonds 2013). As already pointed out in the Introduction, the pollen grains are later unintentionally ingested when the spider eats them along with its old web (recycling of web proteins) prior to constructing a new web (Breed et al. 1964; Peakall 1971; Smith & Mommsen 1984; Townley & Tillinghast 1988; Levi 1997; Blackledge et al. 2009). Unintentional pollen feeding is difficult to observe with the naked eye under field conditions because it frequently occurs during the night (Cloudsley-Thompson 1987); however, this type of pollen feeding could be indirectly proven by means of laboratory techniques (Smith & Mommsen 1984; Ludy 2004; Eggs & Sanders 2013). Smith & Mommsen (1984) have shown in laboratory experiments that the life expectancy of second instar *A. diadematus* spiderlings with access to birch pollen doubled compared to starving spiderlings, providing evidence that the spiderlings did indeed gain nutrition from the trapped pollen grains during the web recycling process. Birch pollen used in this study is

considered high quality pollen because of its high protein content (Roulston et al. 2000). Similarly Eggs & Sanders (2013) have shown by means of a stable isotope analysis that *A. diadematus* spiderlings did unintentionally ingest nutrients from spruce and pine pollen trapped in the spiderlings' webs. In the case of pine pollen, however, this must be viewed with great caution because pine pollen is considered to be low quality pollen with little nutritional value due to low protein content (compare Knop & Hoy 1983; Carrel et al. 2000; Roulston et al. 2000).

Finally, web-building spiders such as linyphiids and theridiids, which do not recycle their webs (Benjamin & Zschokke 2003, 2004; Blackledge et al. 2009), likewise intercept airborne pollen in their webs. Such spiders have been witnessed feeding on pollen grains after plucking them from the web (Meissle & Romeis 2009; Peterson et al. 2010). The behavior of plucking pollen grains from the web and directly eating them (intentional pollen feeding) does sometimes appear in orb-weavers as well (Ludy 2004).

3.4 Spiders as seed feeders.—Apart from plant pollen, tiny airborne plant seeds get caught in spider webs (Dale 1989). For example, hundreds of the minute airborne seeds of the orchid *Cymbidium bicolor* Lindl. (<1mm Ø; Swamy et al. 2004) are sometimes trapped in orb-webs (Anonymous 2010) and it is safe to assume that they are unintentionally ingested along with the old web during the recycling process. There is an anecdotal report by Berland (1933) of an orb-weaving spider, *Neoscona adianta* (Walckenaer, 1802)(Araneidae), sucking a grass seed (Poaceae). This is, so far, the only published report of an instance of seed feeding by spiders. In the laboratory researchers succeeded in raising spiders on a liquid diet manufactured from the large seeds of the soybean *Glycine max* (Fabaceae) (Amalin et al. 1999, 2001).

3.5 Spiders as spore feeders.—In addition to pollen and minute seeds, airborne spores from many different fungal families (e.g., Botryosphaeriaceae, Davidiellaceae, Helotiaceae, Massarinaceae, Microasceae, Nectriaceae, Phragmidiaceae, Pleosporaceae, Trichocomaceae, Trichosphaeriaceae, and Venturiaceae) are blown by wind into spider webs (Smith & Mommsen 1984; Linsens et al. 1993; Bera et al. 2002; Del Fiol et al. 2007; Quamar & Chauhan 2011). The spores collected from webs represent some of the most common fungal genera one would expect to find in air (and which can be identified easily; Kathie Hodge, pers. comm.). As far as is known to us, feeding on fungal material by spiders has never been witnessed in the field; but it has been proven in laboratory experiments that fungal spores sticking to the viscid threads of orb-webs of *A. diadematus* were ingested along with the old web (unintentional spore feeding) just prior to the construction of a new web (Smith & Mommsen 1984). Furthermore, feeding on fungal material by a linyphiid spider was witnessed in laboratory feeding trials (Sunderland et al. 1996). The digestive fluid of spiders does contain the enzyme chitinase needed to dissolve and digest the chitinous spore cell wall of fungi and this explains why spiders are capable of digesting fungal spores (Mommsen 1978a, 1980; Smith & Mommsen 1984). It is still unknown whether unintentional ingestion of fungal spores might benefit spiders. Preliminary feeding experiments conducted by Smith & Mommsen (1984) using spores of *Cladosporium herbarum* (Pers.) Link (1816) suggest that the spores

from this fungus were of no nutritive value to the tested spiders. The suitability of fungal spores in a spider diet is furthermore questionable due to their content of toxic secondary metabolites (Smith & Mommsen 1984; Lundgren 2009). When second instar spiderlings of the orb-weaving spider *A. diadematus* were offered *Cladosporium* spores as potential food, the webs were rebuilt less frequently compared to a control group of starving spiderlings suggesting that the *Cladosporium* spores were either unpalatable or deleterious, so that the spiderlings tried to avoid exposure to them by reducing the frequency of web building (Smith & Mommsen 1984).

Whether cursorial spiders, which encounter fungal spores while wandering over plants, also consume this type of food has not yet been explored. Encountering fungal spores is definitely not without risk for spiders, because there are ~50–100 species of highly specialized fungal pathogens (in particular in the family Cordycipitaceae) whose spores are lethal once they attached themselves to the spiders' integument (Evans 2013). Fungal pathogens cause high mortality in populations of cursorial and web-building spiders in the tropics (Evans & Samson 1987; Gonzaga et al. 2006).

3.6 Spiders feeding on plant material present in the guts of herbivorous prey.—Spiders must also ingest plant material present in the guts of herbivorous prey. For example, linyphiid spiders eating aphids (e.g., Harwood et al. 2004) will also be consuming the undigested (plant sap) and digested (honeydew) plant material within the aphids. Herbivorous prey are therefore likely to be a major source of plant material consumed by most spider species. The evolution of digestive enzymes that can break down this material may have made spiders pre-adapted to feeding on plants directly (for a discussion on spider digestive enzymes see also Mommsen 1978a,b,c,d, 1980; Taylor 2004; Orona-Tamayo et al. 2013).

4. DISCUSSION

4.1 How frequent are incidents of plant feeding?—Feeding on plant materials has been reported so far more frequently from warmer areas (~80% of all reported incidents originating from locations between 40°N and 40°S). This might be due to the fact that a larger number of the reports relate to nectar consumption which has its core distribution in the warmer areas between latitude 0–34° where plants secreting copious nectar are widespread (Pemberton 1998; Chamberlain & Holland 2009) and where nectar can be more easily imbibed due to its lower viscosity at higher temperatures (Lundgren 2009; Nicolson et al. 2013). The most northern occurrence of nectar consumption by spiders refers to a location in Maine (~44° N latitude) and there this type of feeding is apparently scarce (Morse 2007).

4.2 Which spider groups are engaged in plant feeding?—Overall, >60 spider species representing ten araneomorph families have been reported to be engaged in phytophagy under natural conditions (Appendix 1). Six families of cursorial spiders combined, all belonging to the two-clawed *Dionycha* clade (i.e., Anyphaenidae, Clubionidae, Eutichuridae, Salticidae, Thomisidae, and Trachelidae), were attributable to >80% of the reported incidents of phytophagy, whereas cursorial spiders of the three-clawed *Lycosoidea* clade (i.e., Oxyopidae) constituted ~1%. In most cases, spiders reported feeding on plant food were small (including a high percentage of immatures; Smith

& Mommsen 1984; Vogeley & Greissl 1989; Pollard et al. 1995; Jackson et al. 2001; Blüthgen & Reifenrath 2003; Soren & Chowdhury 2011; Pfannenstiel 2012).

One of the most prominent group of spiders engaged in phytophagous activities was Salticidae which accounted for ~60% of all documented incidents (Fig. 1A–D). More than 40 species of salticid spiders, representing a dozen different subfamilies, were observed feeding on plant-derived food in the wild (Appendix 1). The members of this spider family utilize more different types of plant materials as food (including floral nectar, extrafloral nectar, honeydew, plant sap, pollen, and Beltian bodies) than any other spider group. This fits our idea that most salticid species have broad diets and highly flexible foraging patterns (Nyffeler 1999). Furthermore, as mentioned earlier, this family includes the only confirmed species of a specialized plant-eating spider (*B. kiplingi*) known so far (Meehan et al. 2009). Another noticeable group of plant eaters are the group of ‘nocturnal runners’ including the families Anyphaenidae, Clubionidae, Eutichuridae, and Trachelidae (15% of the witnessed incidents; Fig. 1E), whereas flower-dwelling thomisid spiders in the subfamily Thomisinae made up ~11%. The nocturnal runners, composed of fast-moving species, are considered to be the nocturnal counterpart of the diurnal salticids in as much as both spider groups are plant-dwelling cursorial hunters with excellent running and jumping capabilities (Gertsch 1979; Taylor & Foster 1996). But otherwise the two groups differ in many ways from each other, anatomically and behaviorally. A striking difference is the fact that the salticids have excellent vision, whereas the eyesight of the group of nocturnal runners is rudimentary (Jackson et al. 2001). In both groups feeding on plant materials seems to be wide-spread although it must be said that the feeding habits of the nocturnal runners are still largely unknown (Taylor & Foster 1996). The significance of the nocturnal runners as nectar feeders has probably been underestimated in this paper. Though exact data are missing, it can already at this stage be postulated that many of the >8,000 described species belonging to these three spider groups might be engaged in nectarivory at some time of their life history (also see Jackson & Pollard 1996; Jackson et al. 2001; Taylor 2004).

The data presented in this paper suggest that web-building spiders are rather insignificant as consumers of plant food (~13% of the witnessed incidents) compared to the cursorial hunters. However, in reality, pollen feeding by web-building spiders (and in particular orb-weavers) may be more common than shown in this study. Except for a few species hiding in caves and houses (Smithers 2005; Yoder et al. 2009), most cribellate orb-weaving spiders can be expected to trap pollen and other aerial phytoplankton in their webs when it is available. Ecribellate orb-weaver species (with the exception of a small minority of species in the subfamily Cyrtophorinae) all recycle their old web more or less daily prior to rebuilding a new web (Breed et al. 1964; Peakall 1971; Townley & Tillinghast 1988; Levi 1997; Blackledge et al. 2009). Following this logic, we hypothesize that a large percentage of the >4,000 species of cribellate orb-weaver species might derive some nutrients from trapped pollen grains at some point of their life cycle. However, we must admit that it is still unknown what role unintentional pollen feeding plays in the orb-weavers’ energy budget (also see Eggs & Sanders 2013).

4.3 Can spiders survive feeding on only plant food?—The question of whether spiders can survive on a diet of only plant matter was studied in the laboratory using *Bagheera kiplingi* by exclusively offering Beltian bodies as food (Eric Olson, pers. obs.). Although this food was readily accepted, all spiders kept strictly on a Beltian body diet perished after one to several weeks, and always before molting to the next instar, which implies that even this spider, considered by some to be a specialized plant feeder, is incapable of surviving on an exclusively plant diet. These are difficult experiments to perform, however, because the maturation of Beltian bodies is likely to be interrupted by severing Beltian body-bearing leaves from the plant. Results in Mexico, where the spiders feed almost exclusively on Beltian bodies, suggest that when allowed to feed from intact foliage, *Bagheera kiplingi* spiders can survive on a near-exclusive diet of plant material (Meehan 2009; Meehan et al. 2009).

Whether spiders can survive feeding on only plant food was also investigated by offering them an exclusively pollen diet under laboratory conditions. Smith & Mommsen (1984) and Vogeley & Greissl (1989) found that spiderlings of *Araneus diadematus* and *Thomisus onustus* Walckenaer, 1805 kept on an only pollen diet were unable to molt. In these studies, the spiderlings were fed with pollen originating from birch (Betulaceae) and asterids (Asteraceae), respectively. Deficiencies of essential amino acids (e.g., tyrosine) in pollen grains are thought to be responsible for the inability of spiderlings to molt when offered an exclusively pollen diet (Smith & Mommsen 1984; Vogeley & Greissl 1989; Mondal et al. 1998; Praz et al. 2008).

A similar trend was found when spiders were offered an exclusively nectar diet. Anyphaenid and thomisid spiders that received nectar but no prey did not molt in a regular manner compared to insect-fed spiders, and this might be explained by a requirement for protein-rich food in order to molt (Vogeley & Greissl 1989; Taylor 2004). Nectar is known to have a low protein content (Lundgren 2009).

Still another confirmation comes from experiments carried out by Amalin et al. (1999) who fed the spider *Hibana velox* (Becker, 1879) on a ‘soybean diet’ on the one hand and on a ‘milk + egg yolk diet’ on the other. These authors compared the development of the spiders raised on the two diets and found that spiders that were fed an exclusively soybean diet were significantly smaller than those that were fed a milk + egg yolk diet. In another study, Amalin et al. (2001) found that spiders reared on a soybean diet underwent fewer molts compared to spiders reared on a milk + egg yolk mixture. The authors suggested that the delayed development and lower molting success of spiders raised exclusively on a soybean diet might have been caused by some nutritional deficiency (e.g., cholesterol deficiency typical of soybean; Amalin et al. 1999).

It should be pointed out, however, that many generalist predators do better on a diverse diet than they do when restricted to just one prey type (Harwood et al. 2009). This is because predators may gain different nutritional benefits from consuming different types of prey (Mayntz et al. 2005) and/or can dilute prey toxins through eating a mixture of different prey. For example, many linyphiid spiders eat aphids, but when restricted to an aphid-only diet suffer from higher mortality and lower reproductive rates (Harwood et al. 2009). It is not surprising, therefore, that generalist spiders restricted in the laboratory to

a single type of plant food are subject to similar detrimental factors.

5. CONCLUDING REMARKS

Our review reveals that spiders from ten families have been documented to feed on plant products under natural conditions. But evidence based on cold anthrone tests and laboratory feeding studies suggests that spiders from even more families may occasionally consume plant food (e.g., Hajer 1988; Chen et al. 2010; Milne 2010). In the future, the question of whether spiders are eating plants might be tested by means of stable isotopes, or via PCR, using plant (or fungal) primers to detect these materials in their guts. Although this approach would provide evidence of many direct trophic links between spiders and plants there would also be the problem of the indirect links discussed previously, where the plant material was in fact ingested unintentionally through predation on herbivores with plant DNA in their guts. Further work would be necessary to determine the origin of the plant material detected. Pekár & Toft (2015) in a recent review hold the view that alternative foods such as plant materials “often appear to be only marginal foods for spiders and further evidence is required”.

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Appendix 1.—Ninety-three records of spider phytophagy based on visual observation and two records (*) based on stable isotope analyses.

Spider family/species	Food type	Plant family/species	Source
Anyphaenidae			
<i>Arachosia</i> sp.	Extrafloral nectar	Vochysiaceae / <i>Qualea multiflora</i>	Nahas et al. (2012)
<i>Hibana similis</i> (Banks, 1929)	Extrafloral nectar	Anacardiaceae / <i>Anacardium occidentale</i>	Taylor & Foster (1996)
<i>Hibana velox</i> (Becker, 1879)	Floral nectar	Asteraceae / <i>Eupatorium serotinum</i>	Taylor & Foster (1996)
Unidentified	Extrafloral nectar	Euphorbiaceae / <i>Ricinus communis</i>	Taylor & Foster (1996)
Unidentified	Floral nectar	Combretaceae / <i>Terminalia catappa</i>	Taylor & Foster (1996)
Araneidae			
<i>Araneus diadematus</i> Clerck, 1757	Pollen*	Pinaceae / <i>Picea abies</i> , <i>Pinus sylvestris</i>	Eggs & Sanders (2013)
<i>Gasteracantha cancriformis</i> (Linnaeus, 1758)	Pollen	Asteraceae? / Unidentified	Ludy (2004)
<i>Neoscona adianta</i> (Walckenaer, 1802)	Pollen	Unidentified	Gregory (1989)
Unidentified	Seed	Poaceae / Unidentified	Berland (1933)
Unidentified	Honeydew	Pinaceae / <i>Pinus sylvestris</i>	Stephan Scheurer, pers. comm.
Clubionidae			
<i>Clubiona</i> sp. 1	Müllerian bodies	Urticaceae / <i>Cecropia lyratiloba</i>	Jolivet (1988)
<i>Clubiona</i> sp. 2	Floral nectar	Orchidaceae / <i>Neottianthe cucullata</i>	Suetsugu et al. (2014)
<i>Clubiona</i> sp. 2	Pollen	Orchidaceae / <i>Neottianthe cucullata</i>	Suetsugu et al. (2014)
Eutichuridae			
<i>Cheiracanthium mildei</i> L. Koch, 1864	Floral nectar	Asteraceae / <i>Eupatorium serotinum</i>	Taylor & Foster (1996)
	Extrafloral nectar	Euphorbiaceae / <i>Ricinus communis</i>	Taylor & Foster (1996)
Linyphiidae			
<i>Ceratinopsis interpres</i> (O. P.-Cambridge, 1874)	Extrafloral nectar	Sarraceniaceae / <i>Sarracenia purpurea</i>	Marc Milne, pers. comm.
<i>Linyphia triangularis</i> (Clerck, 1757)	Honeydew	Unidentified	Bristowe (1941)
Unidentified	Honeydew	Pinaceae / <i>Pinus sylvestris</i>	Stephan Scheurer, pers. comm.
Oxyopidae			
<i>Oxyopes macroscelides</i> Mello-Leitão, 1929	Extrafloral nectar	Vochysiaceae / <i>Qualea multiflora</i>	Nahas et al. (2012)
Salticidae			
<i>Afraflacilla</i> sp. 1	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Afraflacilla</i> sp. 2	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Asemona murphyae</i> Wanless, 1980	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Bagheera kiplingi</i> Peckham & Peckham, 1896	Beltian bodies	Fabaceae / <i>Vachellia</i> spp.	Meehan et al. (2009) Scully (2012); Eric Olson, pers. obs.
	Extrafloral nectar	Fabaceae / <i>Vachellia</i> spp.	Meehan et al. (2009); Eric Olson, pers. obs.
<i>Bavia aereiceps</i> Simon, 1877	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Chrysilla lauta</i> Thorell, 1887	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Cosmophasis estrellensis</i> Barrion & Litsinger, 1995	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Cosmophasis micarioides</i> (L. Koch, 1880)	Floral nectar	Unidentified	Jackson et al. (2001)
	Extrafloral nectar	Flagellariaceae / <i>Flagellaria indica</i>	Andrea Lim, pers. comm.
<i>Cosmophasis umbratica</i> Simon, 1903	Floral nectar	Rubiaceae / <i>Ixora javanica</i>	Lim & Li (2004)
<i>Cyrba algerina</i> (Lucas, 1846)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Cytaea frontalis</i> (Thorell, 1881)	Extrafloral nectar	Convolvulaceae / <i>Merremia peltata</i> ; Euphorbiaceae / <i>Rockinghamia</i> sp.	Blüthgen & Reifenrath (2003); Nico Blüthgen, pers. comm.
<i>Cytaea</i> sp.	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Diolenius</i> sp.	Extrafloral nectar	Euphorbiaceae / <i>Flagellaria indica</i>	Nico Blüthgen, pers. comm.
<i>Epeus hawigalboguttatus</i> Barrion & Litsinger, 1995	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Eris</i> sp.	Extrafloral nectar	Fabaceae / <i>Chamaecrista nicticans</i>	Ruhren & Handel (1999)
<i>Euryattus</i> sp.	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Evarcha culicivora</i> Wesolowska & Jackson, 2003	Floral nectar	Euphorbiaceae / <i>Ricinus communis</i> ; Verbenaceae / <i>Lantana camara</i>	Cross & Jackson (2009)
	Extrafloral nectar	Euphorbiaceae / <i>Ricinus communis</i>	Cross & Jackson (2009)
	Pollen	Malvaceae / <i>Hibiscus</i> sp.	Nelson & Jackson (2011)
<i>Goleba puella</i> (Simon, 1885)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Harmochirus brachiatus</i> (Thorell, 1877)	Floral nectar	Unidentified	Jackson et al. (2001)

Appendix 1.—Continued.

Spider family/species	Food type	Plant family/species	Source
<i>Heliophanillus fulgens</i> (O. P.- Cambridge, 1872)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Heliophanus debilis</i> Simon, 1901	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Hentzia mitrata</i> (Hentz, 1846)	Extrafloral nectar	Rosaceae / <i>Prunus</i> sp.	Hill (2011)
<i>Hentzia palmarum</i> (Hentz, 1832)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Heratemita alboplagiata</i> (Simon, 1899)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Hyllus gulosus</i> (Simon, 1877)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Lepidemathis sericea</i> (Simon, 1899)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Lyssomanes viridis</i> (Walckenaer, 1837)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Metaphidippus</i> sp.	Extrafloral nectar	Fabaceae / <i>Chamaecrista nicticans</i>	Ruhren & Handel (1999)
<i>Myrmarachne assimilis</i> Banks, 1930	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Myrmarachne bakeri</i> Banks, 1930	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Myrmarachne foenisex</i> Simon, 1910	Honeydew	Unidentified	Collart (1929)
<i>Myrmarachne legon</i> Wanless, 1978	Extrafloral nectar	Rubiaceae / <i>Morinda lucida</i>	Edmunds (1978)
<i>Myrmarachne lupata</i> (L. Koch, 1879)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Myrmarachne melanotarsa</i> Wesolowska & Salm, 2002	Honeydew	Unidentified	Jackson et al. (2008)
<i>Myrmarachne</i> sp.	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Natta horizontalis</i> Karsch, 1879	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Peckhamia</i> sp.	Extrafloral nectar	Unidentified	David Hill, pers. comm.
<i>Pelegrina proterva</i> (Walckenaer, 1837)	Extrafloral nectar	Dennstaedtiaceae / <i>Peridium aquilinum</i>	Douglas (1983)
<i>Phidippus</i> sp. 1	Extrafloral nectar	Dennstaedtiaceae / <i>Peridium aquilinum</i>	Douglas (1983)
<i>Phidippus</i> sp. 2	Extrafloral nectar	Dennstaedtiaceae / <i>Peridium aquilinum</i>	Douglas (1983)
<i>Phintella aequipes</i> (Peckham & Peckham, 1903)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Phintella piatensis</i> Barrion & Litsinger, 1995	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Phintella vittata</i> (C. L. Koch, 1846)	Extrafloral nectar	Malvaceae / <i>Urena lobata</i>	Soren & Chowdhury (2011)
<i>Portia fimbriata</i> (Doleschall, 1859)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Siler semiglaucus</i> (Simon, 1901)	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Tauala lepidus</i> Wanless, 1988	Floral nectar	Unidentified	Jackson et al. (2001)
<i>Xenocytaea</i> sp.	Floral nectar	Unidentified	Jackson et al. (2001)
Unidentified	Extrafloral nectar	Convolvulaceae / <i>Ipomoea pes-caprae</i>	Mondal et al. (2013)
Unidentified	Extrafloral nectar	Vochysiaceae / <i>Qualea multiflora</i>	Nahas et al. (2012)
Theridiidae			
<i>Anelosimus rupununi</i> Levi, 1956	Plant sap	Anacardiaceae / <i>Mangifera indica</i>	Stejskal (1976)
<i>Anelosimus vittatus</i> (C. L. Koch, 1836)	Pollen	Rosaceae / <i>Potentilla</i> sp.	Brian Valentine, pers. comm.
<i>Thwaitesia</i> sp.	Stigmatic exudate	Winteraceae / <i>Drimys granadensis</i>	Marquez et al. (2010)
Thomisidae			
<i>Diaea</i> sp.	Extrafloral nectar	Euphorbiaceae / <i>Macaranga</i> sp.	Nico Blüthgen, pers. comm.
<i>Ebrechtella tricuspidata</i> (Fabricius, 1775)	Extrafloral nectar	Unidentified	Chen et al. (2010)
<i>Misumena vatia</i> (Clerck, 1757)	Floral nectar	Asteraceae / <i>Solidago</i> spp.	Morse (2007)
<i>Misumenooides formosipes</i> (Walckenaer, 1837)	Floral nectar	Apiaceae / <i>Daucus carota</i> ; Asteraceae / <i>Cichorium intybus</i> , <i>Solidago</i> spp.; Lamiaceae / <i>Ocimum basilicum</i>	Pollard (1993); Pollard et al. (1995); Jane Marlow, pers. comm.
<i>Misumenops</i> sp.	Pollen	Apiaceae / <i>Daucus carota</i>	Pollard et al. (1995)
Unidentified	Extrafloral nectar	Vochysiaceae / <i>Qualea multiflora</i>	Nahas et al. (2012)
Trachelidae			
<i>Trachelas similis</i> F. O. P.-Cambridge, 1899	Floral nectar	Asteraceae / <i>Eupatorium serotinum</i>	Taylor & Foster (1996)
	Extrafloral nectar	Euphorbiaceae / <i>Ricinus communis</i>	Taylor & Foster (1996)
<i>Trachelas volutus</i> Gertsch, 1935	Floral nectar	Asteraceae / <i>Eupatorium serotinum</i>	Taylor & Foster (1996)
	Extrafloral nectar	Euphorbiaceae / <i>Ricinus communis</i>	Taylor & Foster (1996)