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Ant-eating twigs and stalks: the natural prey of *Tmarus* and *Monaeses* (Araneae: Thomisidae) in the Western Palaearctic, analysed by using online-accessible wildlife photography

Tobias Bauer

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Abstract. The diet of the Western Palaearctic species of the closely related crab spider genera *Tmarus* Simon, 1875 and *Monaeses* Thorell, 1869 is only little known. A quantitative analysis of images showing spiders with prey, collected from the World Wide Web and the literature, suggests that both genera mainly prey on ants (Hymenoptera: Formicidae), while occasionally capturing other arthropods, such as spiders (Araneae). Most images depict feeding spiders that hold ants anterior-dorsally at the articulation of head and pronotum. *Tmarus galapagosensis* Baert, 2013, from the Galapagos Islands, is known to attack ants by a bite to this region, which, in combination with the photographic evidence, supports the hypothesis that Western Palaearctic representatives of both genera attack ants in a similar way. Three species of *Tmarus* and two of *Monaeses* were identified from the images feeding on ants, demonstrating that probably all species of both genera at least include ants in their diet. In conclusion, Western Palaearctic *Tmarus* and *Monaeses* are myrmecophagous predators and probably have a narrow trophic niche in nature. Furthermore, both genera represent interesting model organisms for the study of trophic specialisation in widespread taxonomic clades.

Keywords: crab spiders, cryptic, myrmecophagy, trophic specialisation

Zusammenfassung. Ameisenfressende Ästchen und Halme: die natürliche Beute von *Tmarus* und *Monaeses* (Araneae: Thomisidae) in der westlichen Paläarktis, untersucht anhand von online frei zugänglichen Naturaufnahmen. Das Nahrungsspektrum von westpaläarktischen Arten der nahe verwandten Krabbenspinnengattungen *Tmarus* Simon, 1875 und *Monaeses* Thorell, 1869 ist nur wenig bekannt. Eine quantitative Zusammenstellung von im Internet verfügbaren Fotografien von Spinnen mit Beute lässt vermuten, dass beide Gattungen hauptsächlich Ameisen (Hymenoptera: Formicidae) erbeuten, während andere Arthropoden wie Spinnen (Araneae) gelegentlich ebenfalls erbeutet werden. Die meisten Bilder zeigen Spinnen, die ihre Ameisenbeute anterior-dorsal am Übergang zwischen Kopf und Pronotum in den Cheliceren halten. *Tmarus galapagosensis* Baert, 2013 ist dafür bekannt, Ameisen mit einem Biss in diese Region zu erbeuten. In Kombination mit den verfügbaren Bildern stützt dies die Hypothese, dass Vertreter beider Gattungen aus der westlichen Paläarktis ihre Beute in ähnlicher Weise attackieren. Drei *Tmarus*- und zwei *Monaeses*-Arten wurden anhand der Bilder mit Ameisen als Beute identifiziert, was aufzeigt, dass wahrscheinlich bei allen Vertretern der Gattung Ameisen zumindest einen Teil der Beute ausmachen. Zusammengefasst kann gesagt werden, dass in der westlichen Paläarktis beide Gattungen, *Tmarus* und *Monaeses*, ameisenfressende Spinnen mit einer wahrscheinlich engen trophischen Nische sind und interessante Modellorganismen für das Studium von trophischer Spezialisierung in einer weitverbreiteten taxonomischen Gruppe darstellen.

This work is dedicated to Elçin F. Hüseynov (Эльчин Ф. Гусейнов, Elchin F. Guseinov/Huseynov) (1973–2021), whose extensive research on the natural diet of crab and lynx spiders greatly facilitated the completion of this paper.

While most spiders are considered opportunistic predators, at least to some extent (e.g. Mezőfi et al. 2020, Nentwig 1987, Pekár et al. 2012), trophic specialisation is only found in a comparably small number of species (Pekár et al. 2012, Pekár & Toft 2015). Crab spiders (Thomisidae) are a cosmopolite, species-rich family (Jocqué & Dippenaar-Schoeman 2006, World Spider Catalog 2021) and powerful predators of various arthropods (Guseinov 2006, Huseynov 2007a, 2007b, Morse 1979, 1981, Nentwig & Wissel 1986, Suzuki 2020). For decades, the ecology and behaviour of flower-dwelling crab spiders has been a subject of intensive research (e.g. Heiling et al. 2003, 2004, Knauer et al. 2018, Morse 1979, 1981, 1983, 1984, 1985, 1989, 1995, 2007, Romero & Vasconcellos-Neto 2004, Weigel 1942), while similar knowledge on other ecological groups of crab spiders, like grass dwellers or arboricolous species, remains sparse and anecdotal. The widespread and species-rich genus *Tmarus* Simon, 1875 is mostly found on branches of shrubs and trees, potentially imitating moss-covered or dried out twigs (Ileperuma Arachchi & Benjamin 2019) or leaf stumps (Roberts 1995), while *Monaeses* Thorell, 1869 mostly inhabits grassland and low vegetation (Dippenaar-Schoeman 1984). Due to their elongated opisthosoma and typical position with stretched-out anterior legs, members of *Monaeses* are perfectly camouflaged to the human eye while sitting on stems or stalks. The genus is probably restricted to Africa and Eurasia, while its Australian species need to be revised and confirmed as members of the group (World Spider Catalog 2021). Recently, Ileperuma Arachchi & Benjamin (2019) demonstrated that *Monaeses* might be a derived group of *Tmarus*, rendering the latter paraphyletic. However, the authors refrained from synonymizing both genera because they argued that a broader taxon sampling of both species-rich groups is needed. Not much is known about the ecology of both genera, but Lubin (1983) analysed the diet of *Tmarus galapagosensis* Baert, 2013 from the Galápagos Islands (sub *Tmarus* cf. *stolzmanni* Keyserling, 1880; see Baert (2013) and the footnote in Lubin (1983: 83)), which was observed to feed exclusively on native ants. Anecdotal field notes on Palaearctic and North American species corroborate the assessment of the genus as myrmecophagous spiders (Guarisco 2007, Kubcová & Buchar 2005, Wunderlich 1995). For *Monaeses*, a quantitative analysis of their diet is absent, but an observation from Sicily suggests a similar myrmecophagous behaviour (Dentici & Amata 2018).

Because both genera are difficult to observe in the field, mostly due to their cryptic pattern and reclusive behaviour (Dippenaar-Schoeman 1984, 1985, Tang & Li 2009), online-accessible wildlife photography of specimens holding prey in their chelicerae provides a valuable source of information on

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the diet of these crab spiders. Therefore, I present an analysis of the natural diet of both genera based on online accessible images from various internet sites and databases and demonstrate that both genera primarily (but not exclusively) prey on ants in their natural habitats.

Material and methods

Images of *Tmarus* and *Monaeses* specimens (Fig. 1, Appendix Tab. S1) were searched by using Google Pictures, in published articles referenced in Google Scholar (search words "Tmarus" and "Monaeses"), the spider forum and Wiki of Arachnologische Gesellschaft (Wiki der Arachnologischen Gesellschaft 2021), the publicly available database of the Iberian naturalist website biodiversidadvirtual.org (Biodiversidad virtual 2020) and inaturalist.org (iNaturalist 2021). Images showing *Tmarus* or *Monaeses* specimens without appropriate metadata in their description (at least a region where the spider was observed) were excluded from the dataset. In case an image showed an ant as prey item, it was determined on which part the spider holds the ant in its chelicerae by applying following three categories: "articulation of head/pronotum", "body" (mesosoma, petiole or gaster) and "legs". In a few images, the position of the bite was not clearly visible and were therefore categorized as "not visible". In some pictures in which spiders and ant prey were depicted from a certain angle, it was possible to take indirect measurements of the body size. This was done using "Makroaufmaßprogramm", a simple software tool that allows indirect measurements in images (Rüdig 2021). Because ants were often bent in pictures, three individual measurements (head with mandibles, mesosoma, petiole + gaster) were taken and added. To allow for comparison with the thresholds for stenophagy used in Pekár et al. (2012), I calculated the Shannon-diversity-index H' (using the natural logarithm) based on arthropod orders.

Several of the images used in the analysis depict specimens determined to species level in the metafiles or accompanying descriptions. These determinations were followed when a) supported by biogeographical and morphological arguments and/or b) accompanied by images of the copulatory organs. The following literature was used to determine depicted spiders: Bosselaers (2018), Dippenaar-Schoeman (1984), Jäger (1995), Levy (1973), Nentwig et al. (2021), Ono (1977) and Roberts (1995). The focus of the study was restricted to specimens photographed within the Western Palaearctic region, because the determination by habitus alone outside this region may not be reliable due to a much higher number of potentially similar (and undescribed) crab spider genera in the tropics and subtropics.

Results

Diet composition and prey size

I found 49 images that show *Tmarus* spiders holding prey items in their chelicerae (H' = 0.298). 46 of all depicted prey items represent (individual) ants (Fig. 1); one image shows a *Tmarus* specimen holding a salticid spider, one a dipteran (Brachycera) and one an unidentified, four-winged insect. In conclusion, non-ant prey items in *Tmarus* images represent 6.1% of all cases in this dataset. For *Monaeses,* 20 images showing spiders with prey in their chelicerae were available (H' = 0.199). In 19 cases, spiders hold individual ants, and in one case (5% of all prey items), an individual *Monaeses* was photographed with an undetermined spider in its chelicerae.

Observed spider species

Three Western Palaearctic *Tmarus* species were identified from available images. *Tmarus piger* (Walckenaer, 1802) (the type species of *Tmarus*) was identified holding ants, a dipteran and a salticid (n = 13). *Tmarus staintoni* (O. Pickard-Cambridge, 1873) was identified from a single image with an ant as prey, the same as *Tmarus stellio* Simon, 1875 (see also Appendix Tab. S1). 19 out of 20 cases of *Monaeses* spiders show *M. paradoxus* (Lucas, 1846), the type species of the ge-

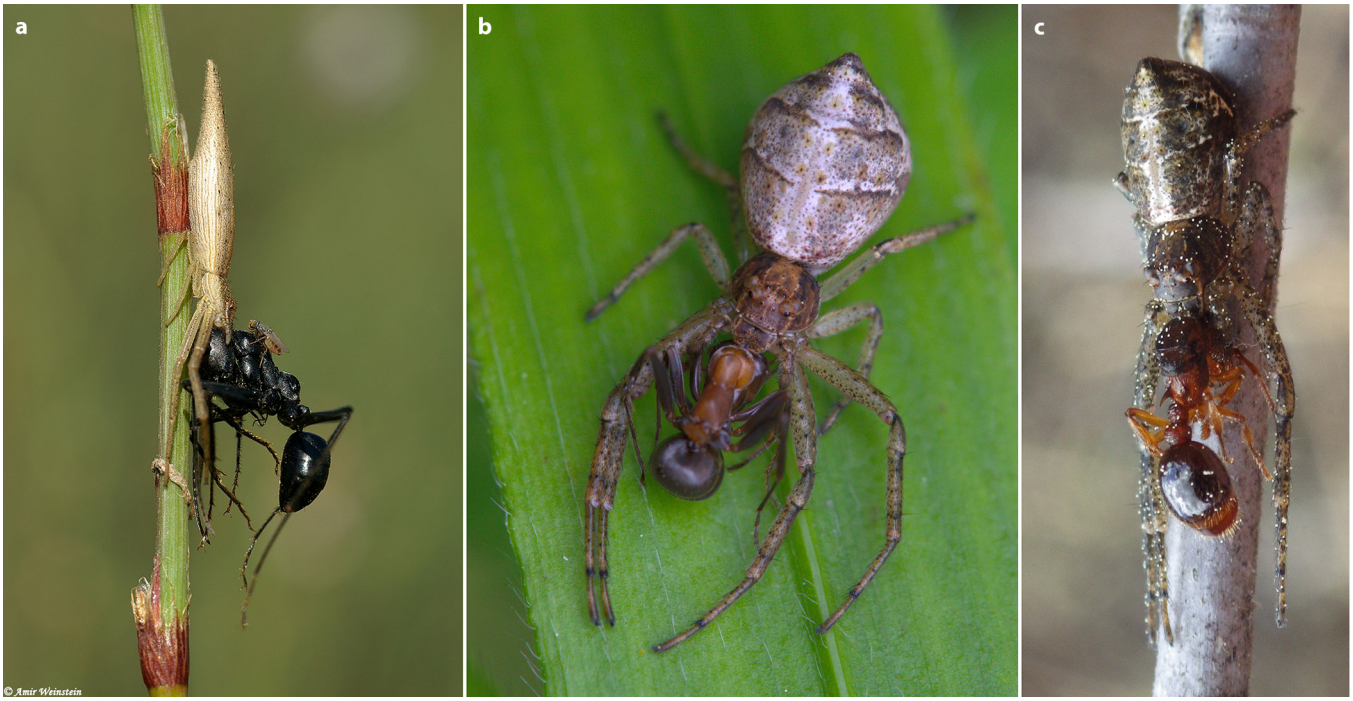


Fig. 1: *Monaeses* and *Tmarus* crab spiders feeding on ants (Formicidae). **a.** *Monaeses israeliensis* feeding on cf. *Cataglyphis* sp. in Israel (photo: Amir Weinstein), a dipteran, possibly a kleptoparasitic member of Milichiidae, is visible on the ant; **b.** *Tmarus* cf. *piger* feeding on cf. *Formica* sp. in Austria (photo: Jürgen Scharfy); **c**. *Tmarus piger* feeding on a queen of the genus *Myrmica* in Brandenburg, Germany (photo: Jonathan Neumann)

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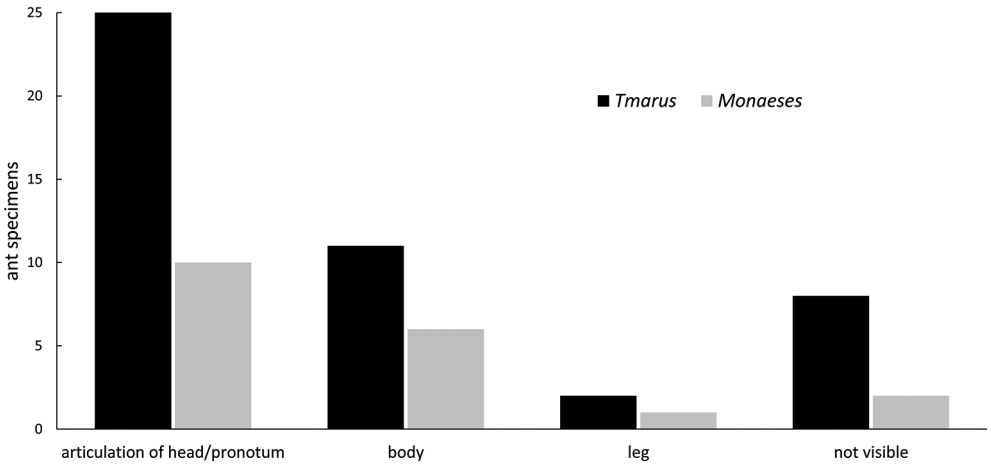


Fig. 2: Position of the bite in *Tmarus* (n = 46) and *Monaeses* (n = 19) crab spiders holding ants in their chelicerae, observed in online-accessible images of feeding specimens

nus, and one shows a female specimen of *M. israeliensis* Levy, 1973 (Fig. 1). The only image with a non-ant prey item (spider) is of *M. paradoxus*.

Position of chelicerae in ant capture

For *Tmarus* (Fig. 2), I found 25 cases of ants held near or at the anterior-dorsally articulation of head and pronotum (cf. Fig. 1), in contrast to 11 incidents were the spider held the ant at a different position on the remaining body. In two cases, the spider held the ant at a leg. In *Monaeses* (Fig. 2), the results were similar. In ten images, the spider held the ant at the area of the articulation between head and pronotum, while in six cases, ants were held at other parts of the body. In one case, the ant was held by the spider at a leg.

Predator-prey size ratio

The ratio of ant body size to spider body size varied in images from 0.99 to 2.16 (n = 7; mean ± SD: 1.43 ± 0.46) in *Monaeses* from 0.84 to 1.26 (n = 4, mean ± SD: 1.1 ± 0.19). On average, both spider genera preyed upon ants that exceeded their own body length.

Discussion

Analysis of prey types

Ants were the main photographed prey in images showing Western Palaearctic species of both genera, *Monaeses* and *Tmarus*. Consulting the thresholds for stenophagy in Pekár et al. (2012), both genera appear as stenophagous in nature ($0 \leq H' \leq 0.3$; but see also Huseynov et al. (2008) and Huseynov (2014). Based on reports in the literature (e.g. Lubin 1983, Wunderlich 1995), this behaviour was to be expected in *Tmarus*. However, the observations show that Palaearctic *Tmarus* also feed on other arthropods, including spiders. A preference for ants over spiders was also observed by Šoltysová (2020) in laboratory experiments with *Tmarus stellio*, but no additional non-ant prey was reported by Lubin (1983) for *Tmarus galapagosensis* from the Galapagos Islands. It is possible that the degree of trophic specialisation on ants in *Tmarus* varies, as observed for the woodlouse-eating genus *Dysdera* Latreille, 1804 (Řezáč et al. 2008, 2021), ranging from euryphagous species to specialists that feed only on a limited number of ant species. Given that *Tmarus* is a widespread and species-rich genus (Ileperuma Arachchi & Benjamin 2019), it might have a similar potential as *Dysdera* for the study of trophic specialisation in spiders, and arthropod predators in general. For *Monaeses*, the observation of Dentici & Amata (2018) already showed that spiders of this genus are potentially able to prey on ants. The data presented here corroborate this hypothesis and suggest that at least *Monaeses paradoxus* is a stenophagous predator of ants in its natural habitat, which occasionally preys on other arthropods.

Lubin (1983) reported that *Tmarus galapagosensis* avoided feeding on introduced myrmicine ants with a sting. In two cases (Appendix, Tab. S1) a *Tmarus* fed on a myrmicine ant of an unknown genus and another was observed feeding on a queen belonging to the genus *Myrmica* that has shed its wings (Fig. 1), which suggests that European *Tmarus* include, at least occasionally, myrmicine ants in their natural diet. However, it is important to note that I did not distinguish between different ontogenetic stages or sexes. It is possible that early instars of both genera prey on a different spectrum of arthropods compared to adults (see e.g. Bartos 2011), which might include a higher number of non-ant insects or other spiders.

Hunting strategy

The majority of images for both genera show spiders that hold ants somewhere at the anterior-dorsal articulation of the head and the pronotum (Fig. 1). Because of their mandibles, sting (most myrmicine ant workers), ability to spray chemicals such as formic acid (formicine ant workers) and cooperative behaviour, most spiders and other arthropod predators avoid preying upon ants (Cushing 2012). Hence, an attack to the dorsal part of the ant's "neck" seems to be a favourable option for a crab spider and keeps the ant's gaster and mandibles away from the spider's body. On the other hand, Foelix (1996) showed that euryphagous crab spiders first attack any available part of the prey's body, and later switch position to the often-observed "neck" hold. Specialised prey capture behaviour, however, evolved independently in different spider groups (e.g. Heller 1976, Jackson et al. 1998, Pekár 2004), which suggests that *Monaeses* and *Tmarus* species might show some specialised behavioural traits towards ants that differ from that of euryphagous crab spider species. Indeed, Lubin (1983, sub. *T. stolzmanni*) reported a very sophisticated hunting behaviour in the nocturnal *Tmarus galapagosensis*. After dropping from a twig to which the spider is still attached by a silken thread, *T. galapagosensis* swings in the air for some time (possibly monitoring ant movements from a

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safe distance) and releases further fine threads from its spinnerets, which become attached to twigs or branches in the vicinity due to light air movements. Then the spider climbs along on one of these threads (and produces a visible dragline), reaches a new position on a different twig or branch and assumes a hunting position. Lubin also speculated that the dragline, which was expanded by one observed spider to a position 2 cm down the twig, might even serve as an alert system. The ant itself is caught by a bite positioned anterior-dorsally of the thorax ("nape of the neck") and the spider later remains in this position while feeding. In addition, the spiders were never observed manipulating prey with their legs. In laboratory trials with *Tmarus stellio* and other crab spider taxa, Šoltysová (2020) observed most often a "head-on" attack on ants in *Tmarus*, in contrast to euryphagous thomisids, which also attacked from the side. This is in accordance with my analysis of images, in which most spiders of both genera held the ants anterior-dorsally somewhere at the articulation between head and pronotum, which corresponds to the observations in Lubin (1983). The spider probably changes the position later (and maybe not in every case) only to feed on other parts of the body, possibly to balance nutrient intake (Pekár et al. 2010). Further, a direct attack to the "neck" of the ant is in accordance with Pekár (2004) as well, who suggested that robust, inaccurate or non-ant mimicking spiders attack ants head-on (like the gnaphosid *Callilepis nocturna* (Linnaeus, 1758); Heller 1976), while more fragile, ant-mimicking spiders like *Zodarion* Walckenaer, 1826 attack from the rear, followed immediately by a retreat. However, there is some variation in the hunting behaviour and position of attack during the ontogenetic development of the ant-eating and ant-mimicking thomisid *Aphantochilus rogersi* O. Pickard-Cambridge, 1871 (Castanho & Oliveira 1997, Oliveira & Sazima 1985). *Strophius nigricans* Keyserling, 1880, another ant-mimicking thomisid, uses dead ants as a protective shield and distraction against living ants, which the spider also preys upon (Oliveira & Sazima 1984). The ant-mimicking *Amyciaea forticeps* (O. Pickard-Cambridge, 1873) also seems to utilize different behaviour to attack its model, *Oecophylla smaragdina* (Fabricius, 1775), but usually attacks from behind (Mathew 1954). Given the microhabitat of *Tmarus* and *Monaeses*, there might be a simple explanation for the frontal attack. Twigs and stalks do not provide the necessary area to perform a sophisticated "attack and retreat" behaviour such as known from *Zodarion*, and bitten prey would simply drop off the twig or stalk on which the spiders sit, and be lost. Hence, the spider has to hold onto its dangerous prey until it is completely immobilised, which happens quickest when a bite is positioned close to the central nervous system.

Predator-prey size ratio

The measurements taken from images suggest that *Tmarus* and *Monaeses* frequently catch ants that have the same or a greater body size than the spider itself. In *Monaeses,* the elongated opisthosoma leads to relatively small ratios between ants and spiders, despite a frequently higher biomass of the caught ant (Fig. 1), so that measurements of the prosoma, which were not possible in available images, probably better reflect the ability of *Monaeses* to overcome large and oversized prey. In summary, this fits to the hypothesis that both genera are specialised ant predators, because stenophagous spiders tend to be able to subdue prey larger than their own body size more frequently (Michálek et al. 2017, Pekár et al. 2014, 2017). Such behaviour is also known from other myrmecophagous spiders (Pekár 2004), with an extreme case of oversized ant prey observed in *Zodarion cyrenaicum* Denis, 1935 (Pekár et al. 2014). However, euryphagous crab spiders are known to be able to frequently catch prey that is much larger than themselves (e.g. Huseynov 2007a, 2007b), which may also include ants (Huseynov 2007b: fig. 2d).

Ant-eating in related groups

Ant-eating behaviour within the Oval Calamistrum Clade (Wheeler et al. 2017) seems to be mostly limited to the Thomisidae and Oxyopidae (e.g. Cushing 2012, Huseynov 2006). Compared to *Tmarus* and *Monaeses*, but also to other crab spiders, some oxyopids inhabit a similar microhabitat. In Azerbaijan, the ant-eating *Oxyopes globifer* Simon, 1876 dwells mostly on *Salsola*-shrubs (Huseynov 2006). Several species of *Tmarus* are often found on branches of shrubs as well (Ilepe-ruma Arachchi & Benjamin 2019, Lubin 1983, Bauer unpubl.). In *Oxyopes lineatus* Latreille, 1806, a lynx spider that inhabits herbaceous vegetation in sunny open areas, ants can represent around 20% of the natural prey (Huseynov 2007c). In *Oxyopes salticus* Hentz, 1845 and *Peucetia viridans* (Hentz, 1832), ants were also found to be part of their diet (Nyffeler et al. 1992). In addition, various species of the lynx spider genus *Hamataliwa* Keyserling, 1887, for instance *Hamataliwa rufocaligata* Simon, 1898, exhibit a similar cryptic colour pattern and possess an elongated opisthosoma not unlike that of many *Tmarus* species (e.g. *Tmarus staintoni*), and are often found sitting on branches (Dippenaar-Schoeman et al. 2020). They resemble small twigs and, on the first glance, might even be mistaken for a *Tmarus* species.

Conclusion

The available images of feeding *Tmarus* and *Monaeses* spiders suggest that both spider taxa are stenophagous ant predators in nature. Although ecological traits often evolve rapidly and do not always reliably reflect phylogenetic relationships (Miller & Wenzel 1995), the similarity in the diet of both genera, and possible deviations in individual species, should be considered and tested in a phylogenetic context and might help to further clarify the relationship between both groups. Future research should also target the hunting behaviour and natural diet of a larger spectrum of representatives from the two genera discussed here. This should include island taxa, species from tropical regions as well as different ontogenetic stages, which might lead to further insights into the evolutionary history and to a better understanding of stenophagy in spiders and other arthropods in general.

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Electronic supplement

Tab. S1: Data and further information on analysed images. Species names in bold represent images in which predator-prey ratio was measured

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