SHORT COMMUNICATION

Functional diversity of ladder-webs: moth specialization or optimal area use?

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Abstract. Ladder-webs are built by several orb-web spider species and can be divided into two main groups based on the microhabitat in which they are built, either in open spaces (aerial) or against tree trunks (arboricolous). In Australian ladder-web spiders, *Telaprocera*, the elongated webs are a highly plastic behavioral response to building in space-limited conditions against tree trunks, while the aerial ladder-webs of *Scoloderus* are an adaptation for catching moths. However, the relative importance of moth capture in the construction of elongated webs in arboricolous spiders cannot be determined with existing data. We here present observational and experimental data concerning prey capture in the arboricolous spiders *T. maudae* Harmer & Framenau 2008 and *T. joanae* Harmer & Framenau 2008. We found that moths make up only a small fraction (< 4%) of the diet of *Telaprocera* spiders and that the proportions of major prey orders in webs are representative of available prey. Our experiments indicate that these webs do not function well at retaining moths. However, further data are required before more definite conclusions can be drawn regarding whether these webs are more effective at retaining moths than standard orb-webs.

Keywords: *Telaprocera*, orb-web, moth, prey specialization

Some orb-web spiders build webs that are specifically adapted to catch moths (Stowe 1986). Typical orbs are ineffective at retaining these prey because the scales covering a moth's body detach upon contact with a web, allowing it to fall to safety (Eisner et al. 1964). The ladder-webs of the genus *Scoloderus* Simon 1887 are highly effective moth-capturing devices (Eberhard 1975; Stowe 1978). On the other hand, the ladder-webs of another genus, *Telaprocera* Harmer and Framenau 2008, have been shown to be a response to space limitation (Harmer 2009; Harmer and Herberstein 2009). However, the importance of moth capture in the construction of elongated webs in *Telaprocera* has not been explored. In this study we investigate prey capture in *Telaprocera* spiders for the first time.

Moth specialization occurs in several genera and is usually associated with a reduction in the orb-web (reviewed in Stowe 1986). The best-known example of web reduction for moth specialization occurs in bolas spiders (e.g. *Mastophora* Holmberg 1876), which hunt using a single strand of silk with a sticky mass on the end and attract male moths within range by mimicking female pheromones (Eberhard 1977; Yeargan 1994). Extension of the orb-web to target specific prey is much less common than web reduction. The exception is the ladder-web of the genus *Scoloderus*. Eberhard (1975) suggested extreme elongation in ladder-webs assists in retaining moths because as they tumble down the web they lose sufficient scales to become entangled. Stowe (1978) confirmed Eberhard's hypothesis by determining that the diet of *S. cordatus* (Taczanowski 1879) consists of almost 70% moths.

Ladder-webs are built by spiders in three different orb-web families (Araneidae, Nephilidae and Tetragnathidae), yet we know remarkably little about the foraging ecology of these spiders. Based on the microhabitat in which they are built, ladder-webs can be divided into two main groups with potentially different functions. The first group, which we here call aerial ladder-webs, includes the araneid genus *Scoloderus* (Eberhard 1975) and the New Guinean tetragnathid *Tylorida* sp. Simon 1894 (Robinson and Robinson 1972). These webs are built in open spaces among the vegetation. Spiders of these two genera build webs that may be over 1 m long (Robinson and Robinson 1972; Stowe 1978), although placement of the hub differs between the two. The hub of *Scoloderus* webs is at the extreme bottom of the web and the hub of *Tylorida* sp. is at the extreme top. It remains to be seen if *Tylorida* sp. is also a moth specialist, although Robinson

and Robinson (1972) suggest the web may target insects with variable flight altitudes.

The ladder-web spiders in the nephilid genera *Herennia* Thorell 1877 (Robinson and Lubin 1979; Kuntner 2005) and *Clitaetra* Simon 1889 (Kuntner 2006; Kuntner and Agnarsson 2009), and the araneids *Cryptaranea atrihastula* (Urquhart 1891) (Forster and Forster 1985) and *Telaprocera* (Harmer 2009) build their webs almost exclusively against tree trunks, hence we refer to them as arboricolous ladder-webs. Web structure varies within the arboricolous ladder-web group. *Herennia* species curve the web around the tree (Robinson and Lubin 1979) while the other species build planar webs slightly offset from the tree surface. The hub position varies from a central position (*C. atrihastula*, *Telaprocera*) to nearer the top (*Herennia*, *Clitaetra*). Evidence indicates that the ladder-webs of *Telaprocera* (Harmer 2009; Harmer and Herberstein 2009), along with those of *C. irenae* (Kuntner et al. 2008), are a response to building webs in space-limited conditions. As these spiders build exclusively against tree trunks, they are limited in horizontal space for web construction. The only way to increase capture area is to elongate the web vertically. Whether or not the other arboricolous ladder-web species also elongate their webs for this reason has yet to be tested.

The differences in fine-scale web structure and web function (moth specialization vs. optimal area use) between aerial and arboricolous ladder-webs suggest they are not convergent structures; however, a moth-capturing function has not been ruled out for arboricolous species. As the highly elongated web structure of *Scoloderus* aids these spiders in catching moths, it is possible that the ladder-web structure of arboricolous species secondarily confers an ability to retain intercepted moths. Among ladder-webs, only the prey of the aerially building *S. cordatus* (moth specialist) and the arboricolous *H. papuana* (generalist) have been surveyed, with moths making up less than 70% and 10% of their diets respectively (Stowe 1978; Robinson and Lubin 1979). Despite strong evidence for *Telaprocera* ladder-webs being the result of space limitation (Harmer 2009; Harmer and Herberstein 2009), we cannot dismiss the possibility of a moth-capturing function in *Telaprocera* ladder-webs without first surveying their prey. In this study we examined whether or not a high proportion of the prey retained by *Telaprocera* webs are moths. We also carried out preliminary experiments to see how long moths are retained and how far they tumble in *Telaprocera* webs. If *Telaprocera*

ladder-webs are adapted for catching moths, we expected that moths would constitute a significant proportion of their natural diet and that a high proportion of moths that contacted the web would actually become ensnared.

Telaprocera **prey.**—The prey of *T. maudae* Harmer & Framenau 2008 and *T. joanae* Harmer & Framenau 2008 were surveyed in Lamington National Park, southeastern Queensland, Australia, in February and July 2006, and March 2007. During the day, we searched for webs on trees and haphazardly selected approximately 30 webs to be surveyed. Since *Telaprocera* are nocturnal foragers, we placed a small colored marker under each web so we could relocate it at night, but the marker had to be removed following each night's survey. This meant that we may have sampled some webs more than once. However, the mean (± SD) number of prey per web per night was 1.18 ± 0.29, and no web caught more than three prey items in a night. Therefore, it is very unlikely that a single web biased our results. For 6 h beginning at sunset, we inspected each web for prey in a circuit-like fashion, so that after the last web was checked we started back at the first web (~ 1 h per circuit). As has been reported for *Eriophora edax* (Ceballos et al. 2005), preliminary surveys also indicated that few insects are captured between midnight and dawn, so we ceased surveys at midnight. We repeated the survey three times over 13 mo, sampling in both summer and winter. On several occasions, we opportunistically observed prey interception in webs during the day, but spiders did not respond to these prey, so we did not systematically survey diurnal prey capture. We collected prey items directly from webs or feeding spiders with a pair of soft forceps, placed them into a vial of 70% ethanol, and identified them to order and noted whether or not the spider had wrapped the prey. For analysis, we pooled prey from both *T. maudae* and *T. joanae*. We have previously shown (Harmer 2009) that the webs of these species are indistinguishable, and we assumed that the two species exhibit similar prey responses. Voucher specimens are deposited at the Queensland Museum.

To compare the actual prey of *Telaprocera* spiders with prey that was potentially available, we set up sticky traps on trees in similar positions as webs (as recorded by Harmer 2009). On each of the nights we inspected webs for prey, we placed 16 traps out just before sunset and collected them six hours after sunset (i.e., the same period webs were inspected). Sticky traps of approximately the same surface area as an adult *Telaprocera* web (~ 300 cm²) were made from an A5 sheet of overhead transparency film coated in Tangletrap (The Tangle Foot Company, USA). We pinned these traps to trees with a small piece of wire that held them slightly off the bark, mimicking a *Telaprocera* web. We transferred prey on traps to vials containing 70% ethanol and later identified them to order.

We collected a total of 169 prey items from webs, 107 of which the spider had wrapped, and 273 prey items from traps. Prey belonged to 16 different orders including insects, arachnids and isopods. Twenty-five prey were unidentifiable as they had been partially digested by the spiders. We only included the most common types of prey (frequency > 3) in the analyses due to very low numbers of some orders. Comparisons between web and trap prey are presented in Figure 1. Diptera, Coleoptera and Hymenoptera were the most common types of prey in both webs and traps, with Araneae, Hemiptera, Isopoda and Lepidoptera making up small fractions of the total (Fig. 1). We carried out two separate analyses comparing the proportion of each individual prey order in webs to its proportion in traps using Fisher's exact tests. First, we compared prey in traps to all prey items collected from webs for each order. Significantly more prey were found in webs than traps for the orders Hemiptera ($P < 0.001$), Isopoda ($P = 0.028$) and Lepidoptera ($P < 0.001$). We then compared prey in traps to only those prey in webs that the spider had wrapped. We found a significant difference in the proportion of Diptera ($P < 0.001$), with many more flies in traps than webs.

Moth retention.—In addition to surveying *T. maudae* prey, we also carried out preliminary observations of moth retention in *T. maudae* webs. To do this, we allowed adult female *T. maudae* spiders to build
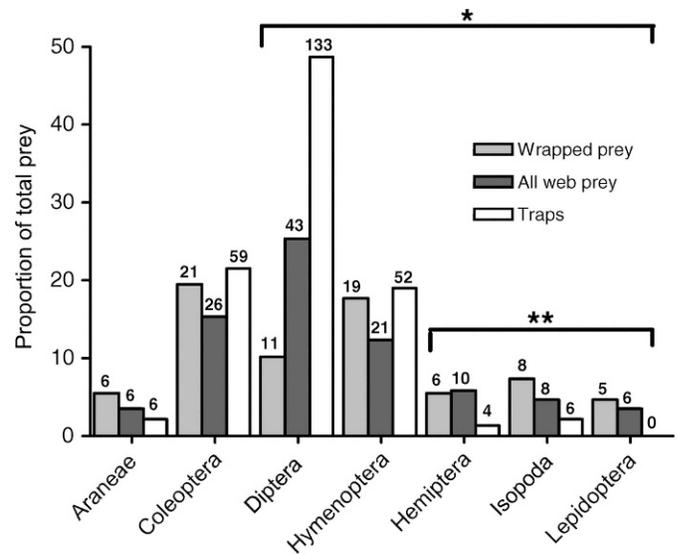

Figure 1.—Proportion of each prey order found in *Telaprocera* webs and in traps. Double asterisks (**) indicate a significant difference in the proportion of prey when comparing all web prey with traps. A single asterisk (*) indicates a significance difference in the proportion of prey when comparing only wrapped prey with traps. Comparisons were made using Fisher's exact tests. Values above each bar are actual counts of each prey order.

webs in frames made from a 50 cm length of PVC pipe cut in half lengthways. Frames were 9 cm in diameter and lined with mesh for the spiders to walk on (see Harmer and Herberstein 2009). We removed the spider after it had built its web, and we used a new spider for each web tested. To test retention, we anaesthetized individual moths (*Plodia interpunctella*; mean length 6.88 ± 0.77 mm) with CO_2 and placed them directly on the web with the long axis of the body perpendicular to the capture threads (i.e., spanning several spiral turns), as close to the top as possible. We repeated this for five moths in each of five *T. maudae* webs ($n = 25$). Care was taken to ensure a fresh part of the web was used for each moth. Although it is not a very natural situation for moths to "wake up" in a web, we used this method to eliminate any differences in the velocity with which prey struck the web and to standardize moth contact with the sticky spiral. We then timed how long it took the moth to escape, from the time it began struggling until it had either completely left the web or 1 min had elapsed. Afterward, we measured the distance the moth had fallen down the web by measuring the length of the trail of scales it left.

The median retention time of moths that escaped *T. maudae* webs was 2 s, range = 1–30 s. Four of the 25 moths did not escape after 1 min. The mean (± SD) distance moths tumbled down the webs was 4.9 ± 2.1 cm. There was no difference in the tumble distances of moths that escaped from those that did not (Mann-Whitney U-test: $U = 36.5$, $P = 0.711$, $n_{escaped} = 21$, $n_{retained} = 4$).

Discussion and conclusions.—We found that *Telaprocera* spiders catch a variety of prey orders with Diptera, Hymenoptera and Coleoptera being the most common. We also found very low numbers of moths in both webs and traps and that *Telaprocera* webs did not function well at retaining moths. These results differ greatly from those found for *Scoloderus* (Stowe 1978) and are likely due to differences in web structure, microhabitat and foraging period between these genera. Our results suggest that moth capture has had little role in the evolution of elongated webs in *Telaprocera* and possibly other arboricolous ladder-web species. This is consistent with previous findings that *Telaprocera* ladder-webs are elongated due to space limitation (Harmer 2009; Harmer and Herberstein 2009).

Moths comprise < 4% of the diet of *Telaprocera* spiders in this study, which contrasts sharply with the almost 70% observed for *S. cordatus* (Stowe 1978). Although there were proportionally more moths in webs than traps, it is unlikely that this difference will have biological significance due to the very low total number of moths over the sampling period (six in webs compared to zero in traps in three weeks of sampling). While moths could potentially be more important energetically or nutritionally than other prey, we cannot draw any conclusions on their dietary importance without first investigating the nutritional value of various prey types. The most common prey orders in both webs and traps were Diptera, Coleoptera and Hymenoptera, although Coleoptera and Hymenoptera probably contributed the most biomass. There was no significant difference in the proportion of these orders in webs or traps when all prey were included in the analysis, indicating that *Telaprocera* webs are intercepting what is most commonly available.

Traps have been used extensively to assess the available prey of spiders (reviewed in Eberhard 1990). However, there are drawbacks in using traps to estimate available prey due to different biases between traps and webs in the types and sizes of prey captured (Eberhard 1990). This point is illustrated in this study where we found significantly more dipterans in traps than webs when only comparing prey that had been wrapped by the spiders. This difference is likely due to the majority of unwrapped prey being tiny flies (≤ 1 mm in length). These flies are intercepted in webs, but they are not "available" to the spiders because the vibrations they produce when struggling are likely to be below the spider's response threshold or because they are not energetically worthwhile for a spider to retrieve. However, spiders could still consume these small flies when recycling the web if they do not escape beforehand. Additionally, our rate of web inspection (~ once per hour) could potentially have underestimated the observed numbers of flies if small flies were caught and consumed between inspections. However, it is unlikely that spiders biased the prey survey by consuming large numbers of small flies between inspections because we observed that they rarely attacked these small prey, although we can not completely rule this out. While there are limitations in comparing prey capture in webs and traps, the lack of moths in webs in this study supports our conclusion that *Telaprocera* are not specializing on these insects.

In our experimental tests of moth retention, only four of the 25 moths failed to escape, and almost 60% of moths escaped in 3 seconds or less. While this could still be enough time for spiders to reach prey close to the hub, prey intercepted near the web extremities may escape before spiders can reach them. However, data on spider attack speeds are required before we can draw any conclusions. The mean tumble distance of moths was only ~ 25% of web length, and there was no difference in the tumble distances of caught or escaping moths, indicating that it was not the length of the tumble that actually retained captured moths. The interaction between moth size and web elongation may also play a role in the retention of these prey. Web elongation will have a greater influence on the capture of large moths than small moths as they are heavier, presumably have more scales and so are likely to tumble further. For small moths that tumble only short distances, an elongated web is unlikely to contribute greatly to prey retention. The length of moths in this study averaged 6.88 mm, similar to the body length of female *T. maudae* (5–7 mm: Harmer and Framenau 2008). Further studies of moth retention in ladder-webs would be improved by comparing different sized moths in webs of varying elongation. Future studies should also compare different prey types and the attack speeds of spiders to see if observed retention times are long enough for spiders to reach prey before it escapes. As our data do not compare the retention times and tumble distances of moths of varying sizes, other prey types, or in other web structures, we are limited in the interpretation of our observations. However, the very low retention rate and short tumble distances, in addition to the low moth capture rate in the field, provide at least preliminary evidence that *Telaprocera* ladder-webs are not adapted for moth capture.

The difference in function between *Telaprocera* webs and *Scoloderus* webs is perhaps due to the very different fine-scale architectures between these two ladder-web types. For example, the radials of *Scoloderus* webs are contorted into a parallel arrangement (Eberhard 1975), whereas *Telaprocera* webs have a more typical radial arrangement (Harmer 2009). It is unclear whether this fine-scale difference helps to retain moths; however, web orientation is potentially more important. *Scoloderus* aerial webs are nearly perfectly vertical, causing moths impacting from either direction to tumble down the web rather than falling out (Eberhard 1975). *Telaprocera* webs generally follow the slope of the tree on which they are built, and if the web is slanted a struggling moth will not fall into lower parts of the sticky spiral, but instead fall to safety. A further possibility for the difference in function is that the capture silks of the two genera differ in stickiness, thus resulting in different moth retention rates.

A final clue to the difference in function between aerial and arboricolous ladder-webs is the difference in the frequency of web replacement and foraging period. *Tylorida* sp. and *Scoloderus* webs (aerial ladder-webs) are built at night and always removed the next morning (Robinson and Robinson 1972; Eberhard 1975). On the other hand, *Herennia*, *Clitaetra*, *Cryptaranea atrihastula* and *Telaprocera* webs (arboricolous ladder-webs) are built at night but not replaced for at least several days (Robinson and Lubin 1979; Forster and Forster 1985; Kuntner 2006; Harmer 2009). This means that aerial ladder-webs are restricted to foraging for nocturnal prey such as moths. Arboricolous ladder-webs can intercept prey both day and night (although their responsiveness to prey in the day may vary) and so have access to a greater prey range.

To conclude, the different forms of ladder-webs, both aerial and arboricolous, all share the common feature of vertical elongation, yet they appear to have divergent functions. *Scoloderus* webs are highly effective moth-capturing devices (Stowe 1978), while elongated *Telaprocera* webs are the result of space limitation (Harmer 2009; Harmer and Herberstein 2009). It will be intriguing to see if the functional difference we observed between *Telaprocera* and *Scoloderus* ladder-webs, paralleling their aerial versus arboricolous microhabitats, holds for the other ladder-web building species.

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