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Short communication

A Bridge Line Web-Pulling Maneuver by the Spiny Orb-Weaving Spider, *Thelacantha brevispina* (Doleschall, 1857)

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ABSTRACT: Relatively little is known about the ethology of orb-web spiders' responses to web-retained, but 'imperfectly' caught, prey. It is generally known that they will either wait for the prey to entangle itself by its own movements and/or shake and tug web radii to produce the same effect. This paper suggests that such pre-attack behaviours may be expressed in more sophisticated ways i.e. are capable of derivation. It describes an observation of the Southeast Asian spiny spider, *Thelacantha brevispina*, in which a complicated, novel web maneuver, elaborated from simple manipulations of radii, was employed in an attempt to retain prey.

KEY WORDS: Araneidae, orb-weaver, prey retention, web

INTRODUCTION

'Imperfect' retention of prey by spider webs is not unusual. Many, or perhaps most, insects actually escape the web before being attacked (Nentwig, 1982; Eberhard, 1990; Blackedge and Zevenbergen, 2006). Likewise a proportion may be rejected for various reasons (e.g. Bristowe, 1941). For those that do not immediately escape and are not summarily rejected, prey interception creates a set of circumstances in which numerous variables (e.g. prey size, likelihood of subduing prey) come into play to determine how or if the spider responds.

The directions and basis for responses to prey may be interpreted in the context of the predictions of Marginal Value Theorem (MVT) (Charnov, 1976) – in which energy expenditure is optimized by favouring quicker energy returns and avoiding increased search efforts that yield diminished rewards. Although originally conceived in spatial terms, MVT may operate at different scales. Thus on customary spatio-temporal scales, a spider may alter its web site in response to prey capture success (e.g. Turnbull, 1973; McNett and Rypstra, 1997; Rittschof and Ruggles, 2010). But equally, the principle can be scaled to web encounters in which conventional foraging parameters like 'patch' are translated into temporal equivalents like web-prey encounter rate and even more specifically, responses to prey web retention.

Probably the most important variables involved in determining responses to intercepted prey, particularly prey which for one reason or another are 'tricky', are the mass and activity of the prey communicated to the spider by web vibrations. For example, grasshoppers (relatively high mass + powerful hind-legs that enable extrication) often get

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caught on web lines, and after various lengths of time, escape. Typically, in such situations the spiders may not respond immediately but wait to see if the prey can entangle itself or escape. These responses are also mediated by the identity of the spiders and the character of their webs – for example, in SE Asia, Leucauge spiders are small to medium sized and generally ignore grasshopper-type catches, while Argiope spiders are larger and often successfully ensnare and consume grasshoppers. Of course, prey type itself varies greatly in identity, with numerous prey variables (e.g. Nentwig, 1982; Hays, 1985) interacting with capture to affect the extent to which insects are held by the sticky capture spiral. Waiting for entanglement is often followed by tugging and pulling at radii from the hub or the section of web with prey to increase the likelihood of capture. This may or may not be the result of communicated information from the web – the spider may be responding to cues that indicate that the prey may be a feasible item that can be turned from an imperfectly caught prey item to a retained item. Alternatively, or perhaps simultaneously, tugging may be used by the spider as a prey diagnostic to determine the degree of retention and resistance in the prey.

These are the predominant pre-attack behaviours observed, but unlike attack and post-attack behaviours which have been well studied in spiders (e.g. Robinson, 1969; Olive, 1980), these sequences have received less attention in the literature. They are well known but they have not been considered to contain much ethological sophistication or diversity. Robinson's (1969) and Robinson and Olazarri's (1971) observations of predatory sequences provided the schemas with which interception behaviours have been traditionally interpreted. In these schemas pre-attack behaviours fit under the categories of prey location and discrimination. They describe 'plucking' of radii as the only behaviour of note. Vieira (2005), for example, separates this a bit further by noting locomotory aspects (to interception site, to hub) as separate units. But essentially there has been nothing to suggest anything else of interest occurs before attack. This refers specifically to observed behaviour – the ways in which prey vibrations communicate information and inform behaviour has been and continues to be a subject of considerable inquiry (e.g. Suter, 1978; Masters, 1984; Landolfer and Barth, 1996; Mortimer *et al.*, 2015).

Pulling on radii is common and well known in spiders that use webs – this includes traditional orb-weavers (e.g. Robinson, 1969; Robinson and Olazarri, 1971), orb-weavers that make non-traditional webs (e.g. Lubin, 1980), and spiders that are not orb-weavers, but make similar types of webs (e.g. Opell, 1979). Likewise, a form of it is probably common in other types of webs also. For example, I have regularly observed pholcids pulling on radii with mosquitoes and small moths. It seems a logical extension of webs and how they and their makers operate. But could there be more behavioural sophistication and/ or diversity in pre-attack behaviours than we are aware of? For example, Nakata's (2010) recent description of radii pulling in spiders waiting for prey, although occurring at an anticipatory stage (before web interception), point to how radial manipulation by the legs may serve multiple functions across the foraging temporal continuum.

Most, if not all, descriptions of prey capture emphasize the importance of rapid responses by spiders to intercepted prey (see Blackedge *et al.*, 2011 and references therein). Imperfect retention encounters are probably less well described because they involve a decision tree of chance in which the most likely outcome is that the prey escapes. Hence there may be a tendency to categorize them simply

as escapes, with their associated behaviours ignored. In the rarer instances when prey is retained then it is usually at the next stage where the success of prey capture is determined; it is usually perceived that the spider receives information that the prey is worth engaging, goes down to its position and attacks. But what if these pre-attack situations are not represented by binary outcomes, but at least three outcomes: (a) prey escape; (b) prey sufficiently subdued/ ensnared for attack; (c) prey still retained but its struggles and identity still indicates that this is temporary. The first and second scenarios are common. The third scenario however generates a decision tree out of the lowest probability. [But not entirely improbable: this is evidenced both by the well-known use of radii tugging and by measures of retention that show considerable variability in prey retention time (Eberhard, 1989)]. Although the initial behavioural sequences connected to this are known, what has not been noted previously is the even rarer outcome, in which a low probability scenario leads to another low probability scenario – i.e. an escalation of uncertainty that is paralleled by behaviours attempting to resolve the uncertainty.

This paper briefly describes a low probability prey encounter in which imperfect prey retention was sufficiently retained for the spider to commit to keeping it in the web, but the imperfect nature of retention forced it to escalate and elaborate its efforts to retain it, culminating in the unusual web pulling behaviour that is the main subject of this paper. To my knowledge, these are novel observations generally, but they are certainly so for this species, *Thelacantha brevispina* (Doleschall, 1857) (Araneidae: *Thelacantha*), a sit-and-wait orb weaving spider, whose biology is almost unknown, except for a study on its barrier webs by Tseng *et al.* (2011).

MATERIALS AND METHODS

Fieldwork was carried out in mixed secondary woodland in the district of Bang Lamung and province of Chonburi, central-eastern Thailand. These observations come from a single prey encounter observed on 3 January 2014 at c. 11 a.m. with air temperatures of 30-35°C and a northerly breeze. The observations were photographed and time signatures from the photographs were used to determine the time-frames of the behavioural sequences. Due to aerial movement of the web many of the photos were out of focus, or were simply not taken because of the need to wait to get the subject in focus, so complete description of each response was not possible. All described observational details were taken from the photos and are meant to convey only what was documented. Thus this note concentrates on the overall sequence of behaviours, their position and main characteristics. Particular emphasis is placed on the novel behaviour seen at the end of the sequence.

Despite hundreds of observations of prey in webs since these specific observations, nothing equivalent to this final behaviour has been seen to date. So the observation remains one of unusual interest occasioned by behaviour and/or conditions that are probably exceptionally rare (see also discussion of low probabilities above). Following on from these observations, attempts were made to replicate similar conditions by placing weaver ants (*Oecophylla smaragdina*) in the webs of *T. brevispina* and another more common spiny spider, *Gasteracantha kuhli*. Although these ants make a good 'resistant' prey owing to their aggressiveness, pilot tests did not solicit the same behaviour, which may be for several reasons – not the least of which is the difficulty of simulating 'imperfect' capture when placing them in their webs. Behavioural observations of this sort may well be worth

pursuing generally, but certainly at the time, the pilot trials were not promising and it was concluded that artificially replicating the conditions leading to the novel behaviour described below was unlikely.

RESULTS

The behavior observed is best considered as a sequence of three connected behavioral responses to prey interception, whose culmination is a complex and previously undescribed web maneuver. The web was approximately 1.5m above the ground and a northerly wind was coming from behind the web (the spider's ventral side). While the spider sat at the hub, a winged apocritan (length = 4mm) (indicated by its narrowed waist) flew into the lower left quadrant of the web (spider's dorsal aspect). It was subsequently determined to be a wasp. No stinger was observable, but it was not possible to tell from the photos whether the stinger was reduced or retracted.

The wasp's attempts to escape warped and stretched the sticky capture spiral immediately surrounding it. The zone of damage was predominantly longitudinal and diagonal – extending widthwise across 4 radii and lengthwise upwards over a grid of 12 capture mesh rungs. There were no broken silk lines observed. So the wasp was imperfectly retained : struggling to escape with sufficient force to warp, but not break the web.

Response 1 (0-1mins): The spider scuttled down the radii to a few centimeters in front of its catch. It assumed an assessment position at a 45 degree angle above the wasp and one radius to the left of the main radius holding the midline of the prey. Then it plucked on the radius ensnaring the midline of the wasp with its right Leg I.

Response 2 (1-3 mins): The spider scuttled back up the radius, it was on back to the hub and proceeded to pull and release the lower radii from the rim of the hub with both Leg Is. This could be seen in the change in localized web tension of the radii immediately above the wasp and leading up to the hub (tautness of vertical radial lines; more acute angles of capture spiral pulled upwards).

Response 3 (3-8 mins): The spider abandoned the hub and climbed up the central radius of the top half of the web, looped a line of silk through the top rungs of the mesh of the sticky capture spiral, positioned itself on the bridge line, pulled the top rungs of the mesh upwards and in so doing tightened the sticky capture spiral taut (Fig. 1). As noted above, I was not able to photograph the entire sequence adequately to note its complete details, but the overall pattern and function of the maneuver can be described. The spider's position on the bridge line was held by contacts with the right and left Legs I, from this position it hung upside down (ventrum facing the sky and tilted upwards on its left side at a 35° angle) in between the bridge line and sticky capture spiral. The spider's dragline was used as a kind of silk 'lasso' with which to tether itself to the upper region of the sticky web mesh. This line was not taut and loosely encircled the upper mesh. To apply pull on the capture sticky spiral the right Leg IV collected the central radius in its claws and pulled upwards (towards the body). The effect was enhanced by picking up the central radius at a point several rungs below the top of the mesh – keeping the upper rungs of the mesh roughly horizontal and unstrained for the tethering lasso and extending the reach of the pull by locating it lower. As the leg lever was drawn towards the body, the sticky capture spiral was drawn upwards toward the bridge line and stretched taut. The spider's body hanging from the bridge line acted as fulcrum for the lever.

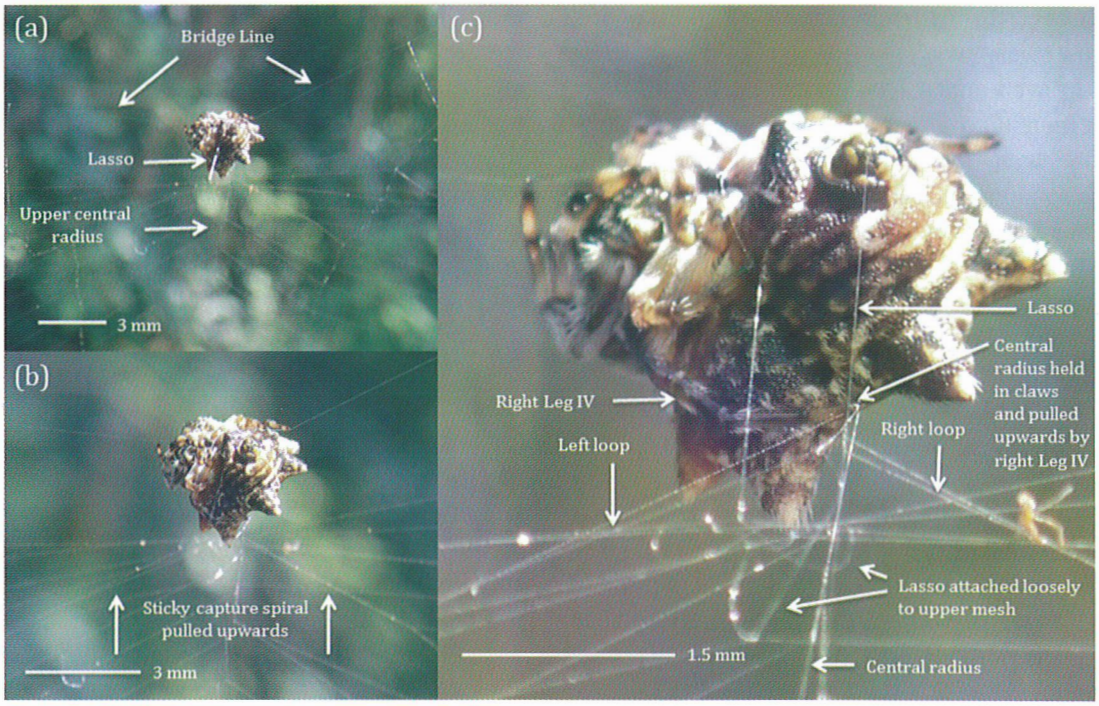


Figure 1. Maneuver used by *T. brevispina* to pull on the sticky capture spiral from the bridge line: (a) – (c) show successive close-ups of the spider resting on the bridge line with the lasso wrapped around the capture spiral. Note the acute angles of the capture spiral threads as they are pulled upwards by the movements of the right Leg IV. (Left and right mesh loops are designated on the basis of the web viewed face-on; the right leg of the spider is viewed in a left position because it is upside down, with the correct designation given for anatomical accuracy).

Loops of sticky capture spiral from the left and right of the upper central radius with junctions close to the point on the radius scooped up by the claws, were also pulled with the radius, creating a compound 'hauling' effect. The extent of pull exerted on the spiral can be seen from the fact that these loops have been pulled out above and outside the orb frame (as represented by the more horizontal unstrained silk lines of the top mesh). The right loop junction was just below the claw. The left loop had a junction that was visually indistinguishable from the radial contact point – i.e. presumably just below the point on the radius that was being held (although it was impossible to determine whether the left loop was directly held by the claws or not). The entire sequence of observations took 8 mins. About 5 mins after the final 'lasso' position was adopted, the wasp escaped.

DISCUSSION

The novel behaviour of pulling on the entire upper quadrant of capture spiral may have worked in two ways: alternations between tugs on the lines, may have created a phased frequency of tightening and loosening that facilitates increased entanglement; or the aim may have been to progressively tighten the silk until the prey is 'locked' into the web. The alternative possibility, that the spider was actually trying to loosen the web and get rid of a prey that was beyond its capabilities, cannot be absolutely ruled out. But it is not

argued for by the escalating effort. Likewise, the wasp was not too large to unbalance the web and it would have been a lot more efficient to either ignore it or cut it out of the web. Its size (smaller than the spider) also suggests that although a wasp, it was a manageable prey item. The change of tugging position and overall escalation of tugged area (localized →lower hemisphere→ entire capture spiral) supports the inference that the three responses represent a sequence of increased effort and force applied to maintain it as prey. Although the final outcome was escape, the fact that this resistant prey was sufficiently retained to not escape for c. 8 mins makes the spider's efforts seem, while perhaps not energetically optimal, consistent with an assessment that its failure to escape quickly, made it a potentially viable prey item.

Why did the spider go to bridge line as its last – and most extreme – resort? When it was, itself, on the web, then any force it applied to pulling on the sticky capture spiral was dampened by the mass of the spider applying a gravimetric pressure on the web in a direction that did not coincide with the location of the prey. The bridge line was the only place the spider could pull on the web without this counteractive effect. The silk lasso provided it with a tether and the right Leg IV pulled on the capture spiral. Without magnification, to the naked eye, the impression was that of a fisherman hauling on a net. The first two attempts to tighten the web applied force to the lower radii. The final novel behaviour applied force to the sticky capture spiral.

Although spiders have mechanisms for avoiding getting stuck in their own capture meshes during the construction phase (see Briceño and Eberhard, 2012), they almost universally avoid contact with it after it has been laid, utilizing radii for movements (it is the radii that are used for travelling along the web plane rather than the sticky lines) and manipulations (it is the radii that are tugged rather than the sticky lines). Indeed, some orb-weaving spiders, that use retreats external to the web, incorporate free sectors without sticky lines into the web plane to enable rapid web movements (e.g. Blackedge *et al.*, 2011). Thus spider body contact with the sticky capture spiral is sparing after the construction phase – hence the need to pull on it indirectly by pulling the central radius. (A small point of contact as represented by the junction of the left loop and the point where the radius was held by right Leg IV would not be a problem firstly due to the small contact area, and secondly because it would limit potential contact to the same zone as that regularly encountered in the sticky capture spiral construction phase). By using silk as an intermediary – both for its primary tether and pulling loci – the spider was able to pull unrestrained on the entire sticky capture spiral and successfully apply tension to the mesh that held its prey.

From an 'optimality' perspective, low probability outcomes should be avoided. However, to distinguish between prey that is sufficiently ensnared for attack and prey that, while still retained, is 'imperfectly' caught and still capable of escape and/or resistance, may mean that the spider must commit to investigating the prey's retention status. It may be that such commitment leads to an abandonment of optimal foraging decisions – i.e. if optimization is structured solely on a wait-act basis, investigation (an act) green-lights all subsequent decisions along an action pathway. This could be one interpretation of the observations described here which are both unusual in character and perhaps excessive in effort in terms of energetic optimization.

Alternatively, the 'rules' by which foraging

decisions are optimized may not apply – deferment of retention is essentially the creation of an unpredictable scenario. In the absence of a pre-existing decision tree the spider may have had to spontaneously make one (i.e. improvise). The observations described here indicate that prey assessment and pre-handling may be extended in unusual circumstances. Although, it is impossible to determine whether this specific instance represented a new experience for the spider, either on this specific occasion or on some other previous similar encounter, the spider observed here constructed an advanced pre-attack decision tree for dealing with imperfectly retained prey.

In that these behaviours followed a clear hierarchic sequence in energetic terms they were internally consistent with an optimality model, even if externally (within the context of successful prey capture) they were not optimal either in terms of energetics or actual outcome. It would be interesting to know how such experience is incorporated into subsequent behavioural decisions – for example, are such behaviours kept as sub-edits in its response repertoire because they represent a new method of web manipulation or does their failed outcome mean that they re-enforce avoidance rules for low probability outcomes? Of course, all considerations of optimality work on the premise that 'if all variables are equal...' – but there are numerous proximate variables that would negate a general optimality approach and could apply to these observations (e.g. spider's nutritional status, previous experience of the site's prey availability, etc). Likewise, 'rules' for prey assessment just may not work all the time – extended duration within a web could potentially equally be interpreted as an increase in the likelihood of prey escape or an increase in the likelihood of prey retention. Whatever the case, *T. brevispina*'s web pulling from the bridge line is a fascinating demonstration of a novel spider-silk interaction that showcases its ability to quite literally think and maneuver 'outside the box' of its own hunting net.

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