Reeling in the prey: Fishing behaviour in an orb web spider

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ABSTRACT

When an insect is intercepted by a spider web, spiders quickly locate the prey, and run towards it. Once they make contact with the prey, they immobilise the prey and retrieve it to the centre of the web or the retreat for consumption. However, in rare circumstances, the spider can also pull the prey towards itself either while running to the prey or from a stationary position, a behaviour termed as 'reeling'. Reeling is paradoxical since it can lead to web deformation or damage, thereby jeopardising future foraging success. Reeling may lead to increased retention time for heavier prey or for information acquisition with respect to the prey's identity, especially when these prey can cause damage to either the web or the spider itself. We explored the function of reeling behaviour in a neotropical orb web spider *Verrucosa arenata*. We show that spiders performed reeling behaviour irrespective whether they were approaching heavy or light prey, but they changed their trajectories of approach. Spiders approached heavier prey slower than light prey and they showed significantly higher frequencies of changes in velocities. We discuss these findings in the context of prey capture strategies and prey recognition.

Key words: spider web, locomotion, predator prey interactions

Introduction

There is an incredible diversity of predatory strategies. These strategies can be grouped into four broad categories based on the predator's method of hunting and their target prey (Curio, 2012). Firstly, some animals (e.g.., octopus, owls) hunt by speculative actions (*sensu* Curio, 2012) that tend to catch unknown prey that are hidden on the ocean floor or among foliage. These predators flush out their prey and catch them as they try to escape. Secondly, predators may choose a particular prey and stalk them till they are brought down, a strategy that is perhaps the most widespread given that it is employed by a wide range of animals from felines to jumping spiders. Thirdly, predators (e.g.., crocodiles, crab spiders) may opt to wait for potential prey to come by and then ambush them, a strategy that conserves energy but has the disadvantage of lack of choice of the identity of the prey on any given occasion. And finally, some predators use external devices such as traps and tools to acquire prey, which extends the catchable range as well as the sensory reach of the organism (e.g., orb web spiders, antlion larvae, crows). However, the physical characteristics of traps and tools add additional constraints to the prey capture process. Trap-using predators are usually sedentary and cannot predict what prey will be captured. Once the prey has been caught and subdued, animals either consume the prey *in situ* or move it to another location to feed their offspring or to protect the kill from kleptoparasites or scavengers.

One of the better studied trap-building predators are the orb web spiders (Eberhard, 1990). These spiders construct a trap made of silk and the spiders wait for prey either in the centre of the web or in a retreat placed to one side of the web. The

spider's foraging success depends on the ability of the web to stop the prey's motion without web breakage, retention of the prey and then finally immobilisation of the prey for consumption (Eberhard, 1990). Additionally, foraging success is influenced by factors such as the structure of the web, the stickiness of the silk, the placement of the web and the interaction between the spider and its web.

Orb web spiders have two choices when faced with the problem of immobilising prey: they can either go to the prey or bring the prey towards themselves. Almost all orb web spiders move towards the prey. In this context, various other constraints created by the web are relevant. The running speed depends on the weight of the spider (Rao et al., 2011); it also varies with the location of the prey (i.e., up or down; (Díaz-Fleischer, 2005)) and the orientation of the spider (Nakata and Zschokke, 2010; Rao et al., 2011).

The second and more unusual strategy is where the spider brings the prey closer to itself, a behaviour known as reeling (Penna-Gonçalves et al., 2009). We can distinguish reeling from other forms of prey retrieval seen in tool using animals such as New Caledonian crows (Bluff et al., 2010). In most other cases, prey is acquired by means of a stick that is inserted into crevices to catch prey and then the entire stick is lifted up and the prey is introduced into the mouth (e.g., Termite fishing by chimpanzees (Van Lawick-Goodall, 1971)). Reeling on the other hand involves the pulling up or rolling up of a flexible structure and the prey is then captured. Reeling as a prey capture strategy is possible only due to the malleable nature of silk and as such is practically unknown in other animals (However, see (Meyer-Rochow, 2007)

for another example seen in fungus gnat larvae, where prey is hauled up after they are caught in bioluminescent mucous silk threads).

Among spiders, reeling is mostly associated with spiders of the families Theridiidae and Pholcidae which have a different web structure compared to orb web spiders (Penna-Gonçalves et al., 2009). Here, under natural conditions, we show reeling behaviour in a neotropical orb web spider, *Verrucosa arenata* (Araneae: Araneidae). We describe the reeling behaviour, analyse the impact of the behaviour on prey capture and hypothesise about the possible costs and benefits. Reeling results in a steady upwards movement of the prey towards the spider. The speed at which the spider approaches the prey caught in the web and the extent to which it reels the prey may depend on the size of the prey. We tested this by comparing spider motion on the web and their trajectories while approaching heavier and lighter prey.

METHODS

Study Species and Site

Verrucosa arenata (Araneae: Araneidae) is a colour polymorphic orb web spider (Rao et al., 2015) that builds webs in the understorey between bushes and trees. This species is sexually dimorphic with females being larger than males (Zschokke et al., 2006). Its distribution ranges from the central United States to Panama (Levi, 1976). *V. arenata* is unusual among araneids because of its upward facing orientation (Rao et al., 2011). We carried out the experiments in urban parks in Xalapa, Veracruz, Mexico, namely the Parque Ecologico El Haya, the Parque Natura and around the

campus of the Universidad Veracruzana. Spiders were released back into the wild after experiments and ethical permission for the use of this species for experimental work is not required according to Mexican regulations.

Characterisation of the reeling behaviour

We located spiders (n = 29) that had built the webs in their natural habitat. Orb web spiders generally complete their prey capture sequence using the following set of behaviours (Robinson, 1971). 1. Plucking, where the spider tugs at the radial threads with their front pair of legs in order to locate the prey or induce further prey movements to facilitate location and retention. Plucking may or may not be accompanied by a shake of the whole body of the spider and can be omitted in the case of rapidly moving prey; 2. Moving rapidly to the location of the prey; 3. Biting the prey and wrapping the prey with silk, or wrapping first and then biting the prey to immobilise it.; 4. Transporting the prey back to the hub for consumption. In the case of *V. arenata*, spiders pluck the web, accompanied by whole body shakes ('bouncing') and then pull on the radial thread ('reeling') as they approach the prey. Reeling may be done from a stationary position en route to the prey or during the approach.

To elicit the reeling behaviour in them, we used the Mexican fruit fly *Anastrepha ludens* (Diptera: Tephritidae) as a model prey species. We carefully placed live flies on the lower part of the web and ensured that the insect was stuck to the web. We filmed the movement of the spider towards the prey using a SONY digital video camera set at 30 fps. In order to describe the leg movements, we filmed one spider at

120fps using an iPhone 6s (Apple, Inc) along with a 3cm strip of paper for scale information placed in the camera's field of view. On each frame, we digitised the head position of spider and fly using a custom written software (courtesy Jan Hemmi and Robert Parker) in Matlab to extract x,y coordinates. We determined the distance between the two animals using their head positions and also calculated their speeds. For these analysis, we considered each prey capture event from when the spider turned to face the prey up to when the spider made contact with the prey with its legs. Coordinates were then exported for further analysis (see below). Each spider (i.e, including its web) was tested once with one fly (Table 1).

Effect of prey weight on reeling behaviour

In order to generate prey with different weights, we affixed a small pellet of non-toxic quick-hardening plastic ('Sugru', FormFormForm Ltd, UK) to the thorax of flies. The weight was added to ensure that heavy flies (n = 14) weighed twice as much as a normal fly (hereafter referred to as 'light prey' (n = 13)). Modified flies retained sufficient wing movements needed to trigger the spider response. We filmed the interaction as described above with a new set of spiders. Spiders were chosen for treatments in a random order and each spider was tested once with one fly of either treatment. In this experiment, flies were only placed on the central downwards radial in order to standardise fly location. We digitised the trajectories and noted down the frame number (i.e., time). We only used the Y coordinate value (i.e. vertical movement) of both spider and fly position since there wasn't any substantial horizontal motion. We did not quantify web damage. Spiders were

subsequently brought to the lab for weight measurements. There was no significant difference in spider weights between the two treatments (t test; df = 1,25, n = 26, p = 0.95).

We analysed the data in two distinct ways. Firstly, we compared the entire trajectories of spiders approaching prey and categorised them (see below). Secondly, we determined the vertical velocity profile of the spiders.

Trajectory Data Analysis

Analyses were carried out in R ver 3.3 (RCoreTeam), JMP PRO ver12, Mathematica ver 11 and Matlab 2015a (Mathworks, Natick USA); (Table 1). We compared the entire trajectories of the spiders as they approached heavy and light prey with a time series analysis. We normalised the y axis points from 0-1 so that all trajectories had the same range, using interpolation. Due to this normalisation, factors such as different web sizes between individuals can be resolved. Similarly, we normalised the time axis from 0 to 1 to facilitate comparison between trajectories. We also categorised the trajectories with an unsupervised cluster analysis using the Dynamic Time Warping technique ('DTW'; Sardá-Espinosa, 2017) in Mathematica. DTW is a measure of the similarity between two time-series trajectories that takes into account the shape of the curves. The results were plotted in the form of a dendrogram.

Positional correlations

We evaluated the correlation between spider and fly position by normalising the x axis (by time) and the y axis (by distance, such that the origin was at the hub position). We divided the x axis into 6 equidistant segments for both spider and fly trajectories (see Fig 5A). We calculated Pearson correlation values within these segments. To test whether the correlation values was determined by the fly treatment (Heavy or Light) and the order of the segment, we conducted an ANOVA. A positive correlation indicates that the spider and fly are moving in the same direction, whereas a negative correlation implies that the fly is being raised up while the spider descends in the web.

Velocity profiles

We tested whether spiders ran faster or relatively different distances towards differently weighted flies using the t-test. One outlier was removed for the heavy fly treatment for the distance analysis. We further tested whether spiders responded to differences in prey weights by adjusting their velocities as they made their way down the web. Velocity changes in spiders can be a result of two types of motion; the first being the bouncing motion made when spiders plucked the web to locate the prey, and secondly when they go down the web. The downward motion was not uniform and there were frequent pauses where the effective velocity of the spider was essentially zero, suggesting that the spider was momentarily at rest. Here we suggest that these fluctuations, i.e., the frequency of pauses during the prey

approach motion, can be considered as a measure of the spider's uncertainty regarding the capture potential of the prey. We used the frequency of pauses as a proxy of the uncertainty demonstrated by the spider in its approach to the prey. In our representation, spiders that show more frequent records of zero velocity would be considered as 'less certain' spiders, whereas spiders that show velocity below zero (negative values since the spider is moving downwards) are 'more certain'. The velocity frequencies of spiders approaching heavy prey and light prey were plotted as a histogram with a probability distribution function fitted onto them. We used a Kolmogorov Smirnov test to evaluate whether there were differences in the distributions between the treatments.

RESULTS

Characterisation of the reeling behaviour

On detecting the prey, the spiders performed a turning motion in order to orient themselves to face the location of the prey. Subsequently, they started pulling the radial thread with their first couple of pairs of legs (i.e., pairs I and II) thereby deforming the structure of the web. During this motion, they reeled in the radial thread such that the entangled prey rose up towards the spider (Fig. 1, Fig. 3; also see Supplementary material S1). Spiders travelled a mean of 0.76 (range: 0.44 - 0.92; n = 29) of the proportional distance to the prey. Spiders could perform the reeling

behaviour either in a stationary position or *en route* to the prey but was most commonly carried out as the spider approached the prey (24 out of 27 individuals).

Time series analysis of trajectories

The spiders used three distinct strategies as they approached the prey. Of the total 27 spiders, some ran down towards the prey with short pauses (8 individuals), whereas other spiders paused for a long time before making the run (3 individuals), while others paused only when they were closer to the prey (16 individuals). We next compared the shape of the trajectories (using y-coordinates) when spiders approached Heavy- and Light-prey. The trajectories fell into three distinct clusters (Fig. 2): Mostly heavy, Heavy outliers (i.e., Heavy flies that spiders responded to in an atypical manner) and Mostly light.

In Figs. 3, 4A and B, this variation was shown as a time series trajectory. The distance between the spider and the prey decreased with time, but the upward motion of the prey was apparent in the end of the curve. In spiders approaching Heavy prey, there were significantly more plucks (seen here as sudden clusters of change in spider position). However, it is also apparent from the figures as well as the dendrogram seen in Fig. 2, that the majority of the variation in the Heavy treatment was contributed by 4 individuals, suggesting that spider response to differential prey weights can be better explored by changes in velocities rather than the shape of the trajectories.

Spiders were significantly slower while running towards heavier prey (t-test; t = 5.27, df = 17.34, p < 0.001). Spiders travelled a shorter proportional distance while approaching heavier prey (Mean ± S.E; 0.70 ± 0.03) in comparison to lighter prey (Mean ± S.E; 0.77 ± 0.03) but this difference was not significant (t-test; t = 1.87, df = 24, p = 0.072). Actual distances (Mean ± S.D. cm; Heavy prey : 6.14 ± 3.96, Light prey : 5.89 ± 2.94) travelled are presented in supplementary material S2 and S3 in more detail. Spiders plucked the web more when approaching heavy prey in comparison to light prey (t-test; t = -2.18, df = 25, p < 0.05).

Positional correlations

There was a significant effect of the model on the correlation values (Table 2; Fig. 5B). However, only the segment order significantly affected the correlations, suggesting that spiders reeled up both Heavy and Light prey but this was more apparent in the final segments (Fig. 5B).

Velocity profiles

Spiders differed in the frequencies of changes in velocity as they approached prey (Fig. 6). We compared the frequency distribution of velocities of spiders approaching heavy and light prey (See example plots in Fig. 6A and B). Here, we considered the fluctuation in velocities as an indicator of spider uncertainty towards the prey; i.e. spiders that were moved regularly towards the prey showed fewer pauses (fewer frequencies of 0) compared to spiders that moved irregularly. The probability distribution fit both the datasets, with a marked peak at 0 for the heavy

prey and a much smaller and flatter peak skewed to the left of 0 for the light prey (Fig. 6C). The distributions of the two data sets were statistically different (Kolmogorov Smirnov test, test statistic = 0.172, p << 0.001).

DISCUSSION

Verrucosa arenata spiders are able to reel in prey from the bottom of the web towards themselves. This behaviour differs according to the weight of the prey, and spiders modified their strategy in accordance to the weight of prey in the web. We observed three main trajectories: (a) spiders might wait and pull the threads after locating the prey and subsequently run towards the prey; (b) spiders might run immediately towards the prey while pulling along the way; (c) some spiders pause and pull the prey towards them at a much closer distance to the prey.

We found significant differences in the velocities of spiders as they approached the two types of prey. Spiders that approached heavier prey showed more fluctuation in their positions as they made their way down the web. This fluctuation can be attributed to two factors: firstly, a plucking motion that has generally been associated to the spider locating the prey (though there may be other functions, such as further entanglement (Robinson and Mirick, 1971)), and secondly the general motion of the spider as it walks down. This motion is not uniform, it consists of several plucks and pulls which cause the spider to have three velocity phases; moving upwards, moving downwards and at rest. In this study, we used the

frequency of state changes as an indicator of the spider's uncertainty of the identity of the prey. We would expect that spiders that are more uncertain about the identity of the prey, as in the case of dangerous prey, should experience more fluctuation in velocities which would lead to a peak at zero since the velocity values would flip from going upwards to downwards (as well as accelerating and decelerating) during the hunting process. We argue that lighter prey were recognised as prey that can be easily subdued and heavier prey are considered as dangerous or problematic prey and therefore need to be approached cautiously. This argument is corroborated by the significantly higher number of plucks, the slower speed to approach, frequent velocity state changes and higher pulling distance. However, we also note that differences in plucking behaviour may be linked to the activity level of the insect itself; in *Nephila clavipes* plucking was more commonly seen when spiders approached insects that were vibrating spasmodically or were still, whereas in insects that were continuously vibrating, the prey was approached directly (Robinson and Mirick, 1971). The resolution of our videos doesn't allow us to tease apart this issue, but we should be able to do so in future experiments.

Reeling in prey has been reported earlier in manipulated webs in order to place this behaviour on a phylogenetic position (Penna-Gonçalves et al., 2009). The reeling behaviour seems to have been retained in orb web spiders even though they do not use these movements for prey capture, while they may use similar behaviour in other contexts such as reeling in silk during web construction. One obvious reason why orb web spiders may not employ this behaviour for capturing prey (they usually move towards the prey) is that reeling may result in web damage and

deformed webs. In an Amazonian orb web spider (*Hingstepeira folisecens*) that builds a retreat in a leaf placed in the centre of the web, a similar behaviour has been reported (Rito et al., 2016). This spider typically waits for prey in the shelter provided by the leaf. When prey land close to the shelter (but not further away), the spider plucks at the strands such that the prey approaches the spider. It has been suggested that in this species, spiders may choose to pull the prey in order to minimise time spent out of the shelter where they are more vulnerable to predators (Rito et al., 2016). However, since the reeling behaviour results in web damage, these spiders are thought to prioritise immediate security over future foraging success.

What are the possible benefits to reeling that outweigh web damage and consequent lost foraging opportunities? In spiders such as *H. floriscens*, reeling in prey occurs mostly when the prey is very close to the shelter, but in other orb weavers that wait at the centre of the web, there is no immediate benefit in terms of protection. We suggest that spiders such as *V. arenata* may reel in prey to entangle them further and prevent escape. The time insects spend caught in the web (retention time) is an important component of web function (Zschokke et al., 2006). Many insects escape from the web after interception simply by struggling strongly (e.g., large bodied insects such as beetles), or by discarding scales (e.g., moths and butterflies). By reeling in prey, spiders can be assured that these insects can be captured since they would potentially stick to various different elements of the web. However, our results showed that spiders change strategy in accordance to the weight of the prey, with spiders running slower towards heavier prey and pulling these prey higher. Furthermore, they adjust their rate of approach and number of

web pulls in accordance to the prey type. This suggests that spiders move irregularly towards heavier prey since heavier prey could be more challenging to subdue either through the defensive capabilities such as stings or strong legs (Eberhard, 2014). Therefore, reeling could be used to ensure that there is no damage inflicted on the spider by struggling prey.

It is uncertain why this behaviour is not seen in more orb web spider species. *Cyclosa spp.*, for example, have been reported to pause and pluck at web strands *en route* to the prey, but this is thought to aid in prey location rather than retrieval (Nakata and Zschokke, 2010). As a representative example, we mapped the prey capture trajectory in a non-reeling spider *Argiope argentata* as it approached a *A. ludens* fly (Fig. 7). The position of the fly at the beginning of the prey capture sequence remained similar at the time of first contact, illustrating that this spider did not pull up the prey. Also noticeable was a lack of distinct plucking movements suggesting that there were few or no pauses during the spider's descent. In *V. arenata*, the webs are usually taken down by the spider or severely damaged by midday due to frequent rainfall during the spider season (pers. obs, Rao, D). Therefore, web damage associated with insect reeling may not be critical when compared to the successful capture of a prey. Another feature of *V. arenata*'s webs is that the silk strands that make up the web are tougher and stretchier in comparison to orb web spiders of similar sizes (Sensenig et al., 2010), but since they build large sparse webs, these spiders may have relatively lesser stopping potential. Therefore, *V. arenata* may be able to reel in prey simply because its web can withstand deformative pulling at a much higher rate than other spiders. These ideas need to be

tested further to tease apart the interaction between reeling in behaviour and web structure. It is also worth noting that the reeling behaviour only occurs when the spider is moving towards a prey that is on the lower part of the web (Rao et al., 2011).

In this study, we explored the reeling behaviour in an orb spider and its possible function. However, it still remains to be seen why this strategy has been adopted in this species and identify the elements of the spider web that allow for the expression of this behaviour. Similarly, any changes in the occurrence of reeling with ontogeny would indicate different strategies at different ages, reinforcing the notion of the spider web as an active component of foraging in spiders rather than a passive aerial trap.

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AUTHOR CONTRIBUTIONS (CRedIT roles, https://www.casrai.org/credit.html)

DR: Conceptualisation, Investigation, Formal analysis, Methodology, Visualisation, Writing – original draft, Writing – review & editing

HTM: Formal analysis, Visualisation

AN: Formal analysis, Visualisation, Writing – review & editing

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Figures
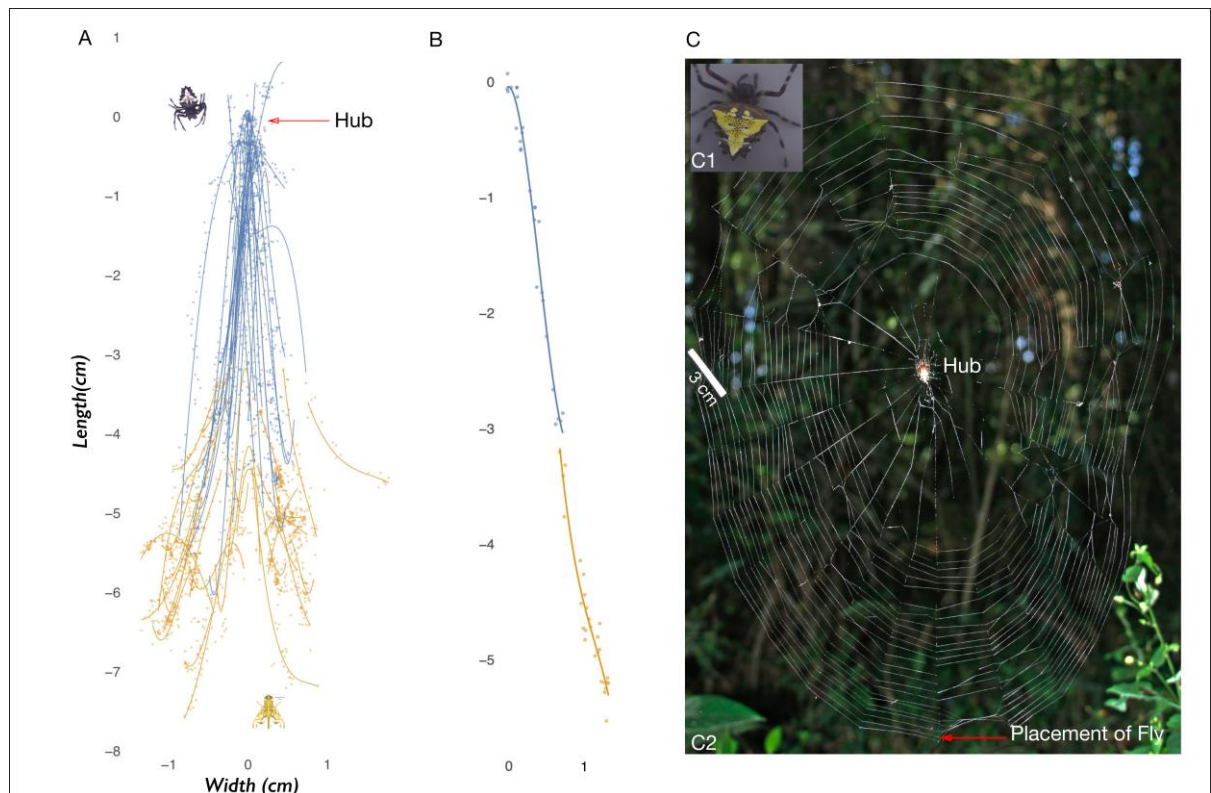
Figure 1: A. Trajectories of *Verrucosa arenata* spiders (blue lines and points) running down towards the prey from the hub position. The movement of the prey (*Anastrepha ludens*) is indicated with yellow lines and points. The points are connected by means of a spline fit to aid in visualisation. B: A single sample trajectory showing the extent of prey movement in the web. C: *Verrucosa arenata* (C1) web showing position of prey placement for the prey weight manipulation experiment (C2; see text for details).

Mostly Heavy

Heavy Outliers

Mostly Light

Height (cm) (normalized)

Time (normalized)
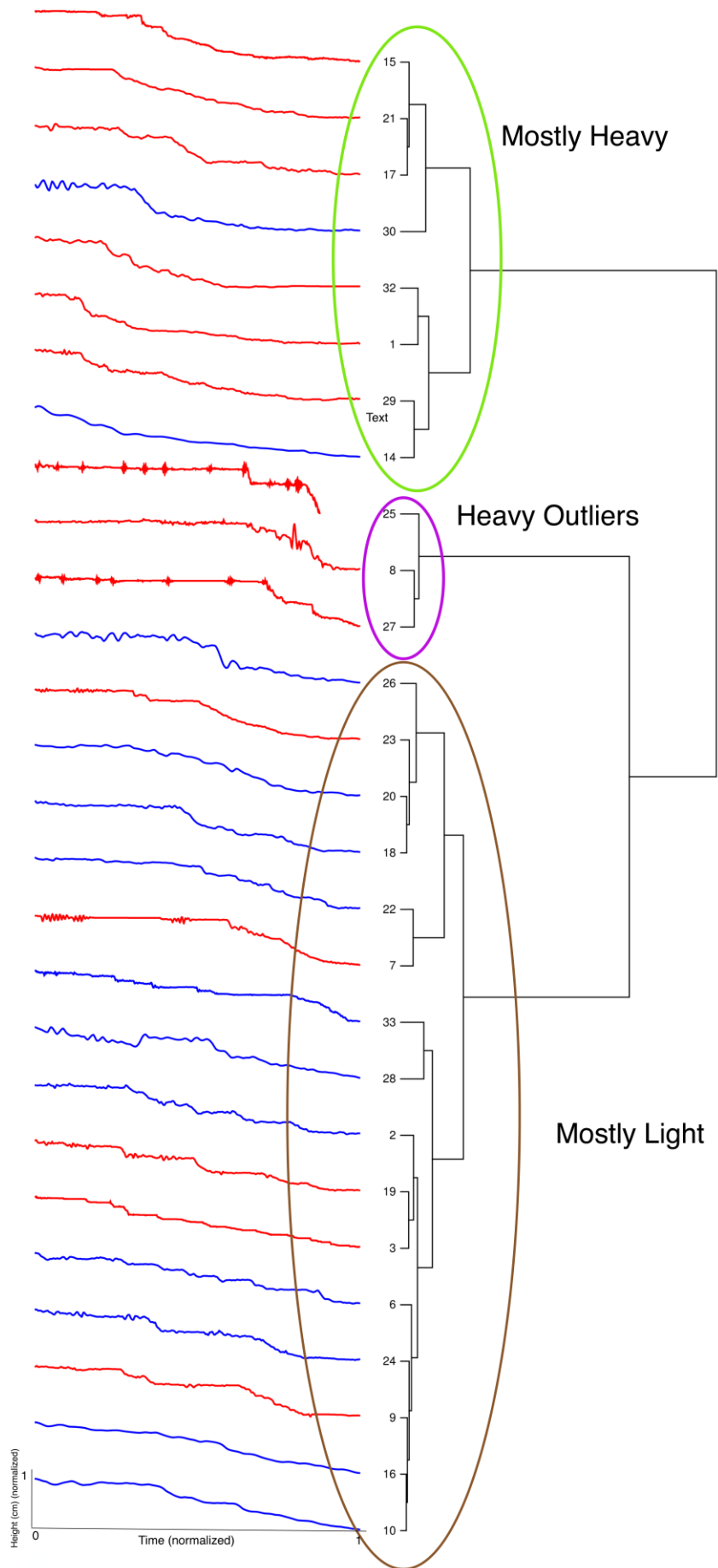
Figure 2: Dendrogram showing the result of an unsupervised cluster analysis based on curve comparison using the Dynamic Time Warp technique of the Y axis trajectories (i.e., change in height) of the spiders that approached Heavy prey (red lines) and Light prey (blue lines). The trajectories largely fall into three categories that can be designated as Mostly heavy, Heavy outliers and Mostly light. The X axis of the trajectories is the length of the prey capture sequence in time; all trajectories have been normalised (from 0-1 in both axes) for curve comparison. Numbers attached to the dendrogram are spider identity numbers.
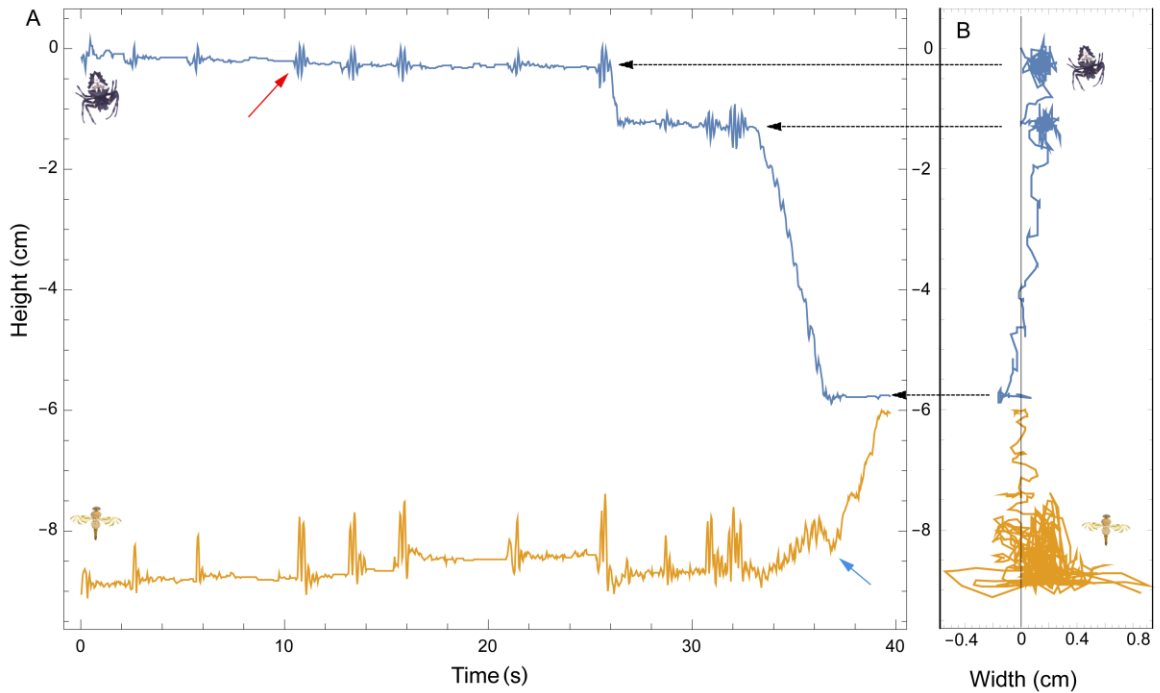
Figure 3: A. A sample trajectory of a *V. arenata* spider (blue line) as it approached the prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis represents the time taken for the spider to make contact with the fly. The red arrow shows the fluctuation in spider position caused by the spider plucking the web. The blue arrow shows the point when the spider starts reeling in the fly. B. A sample trajectory of the prey capture sequence seen with both X and Y components of the trajectory. The black arrows show the corresponding position of the spider during the plucks and the reeling.
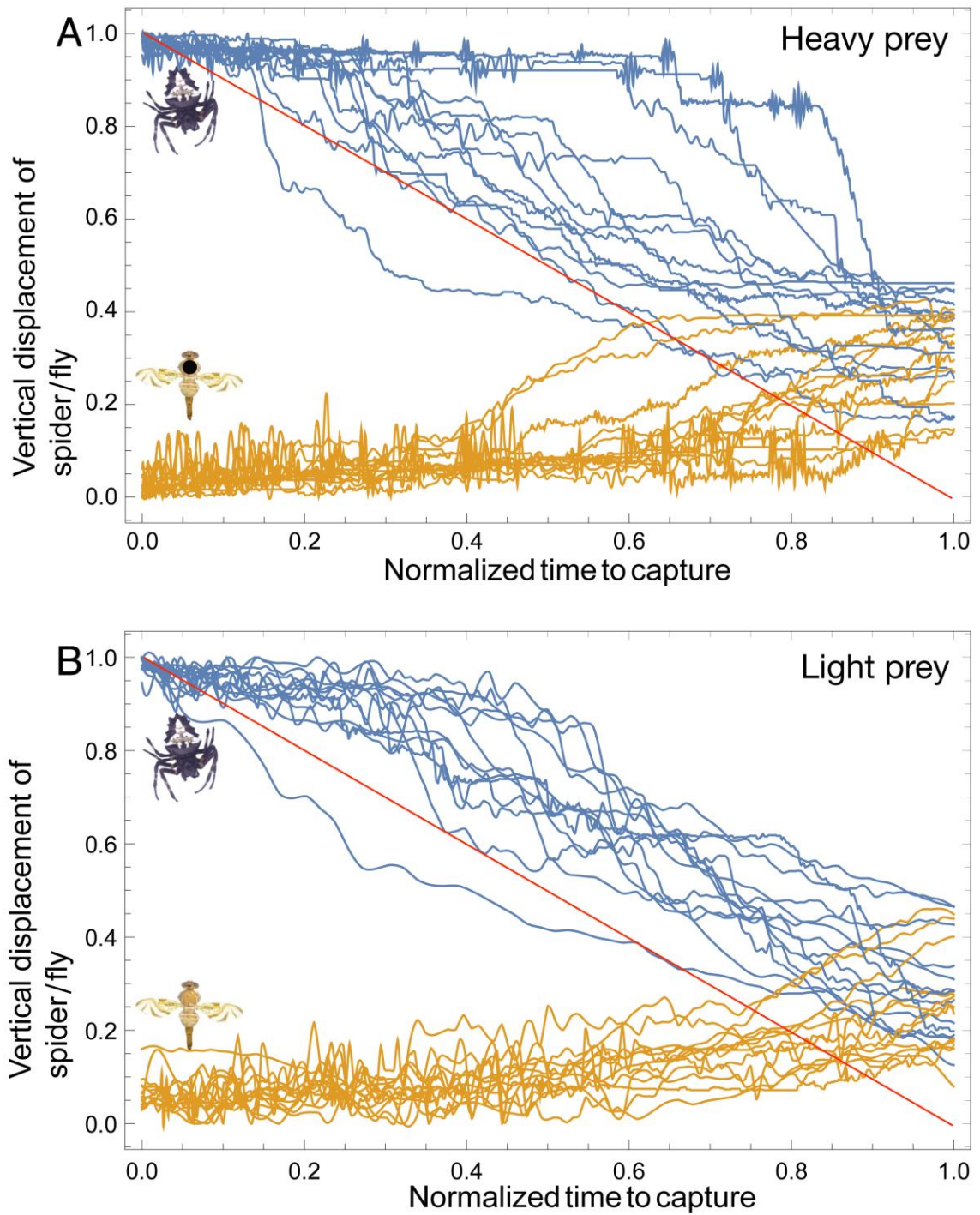
Figure 4: All trajectories of spiders approaching Heavy prey (a tephritid fly shown with a black circle on the thorax; A) and Light prey (B). The trajectories are represented as normalised time series curves with the Y axis as the normalised

vertical component of relative positions of the spider (blue lines) and fly (yellow lines), and the X axis as the normalised time during the prey capture sequence. The red diagonal line represents the hypothetical path taken by a non-reeling orb web spider that runs at a constant speed. See supplementary material S2 and S3 for trajectory plots of individual pairs.
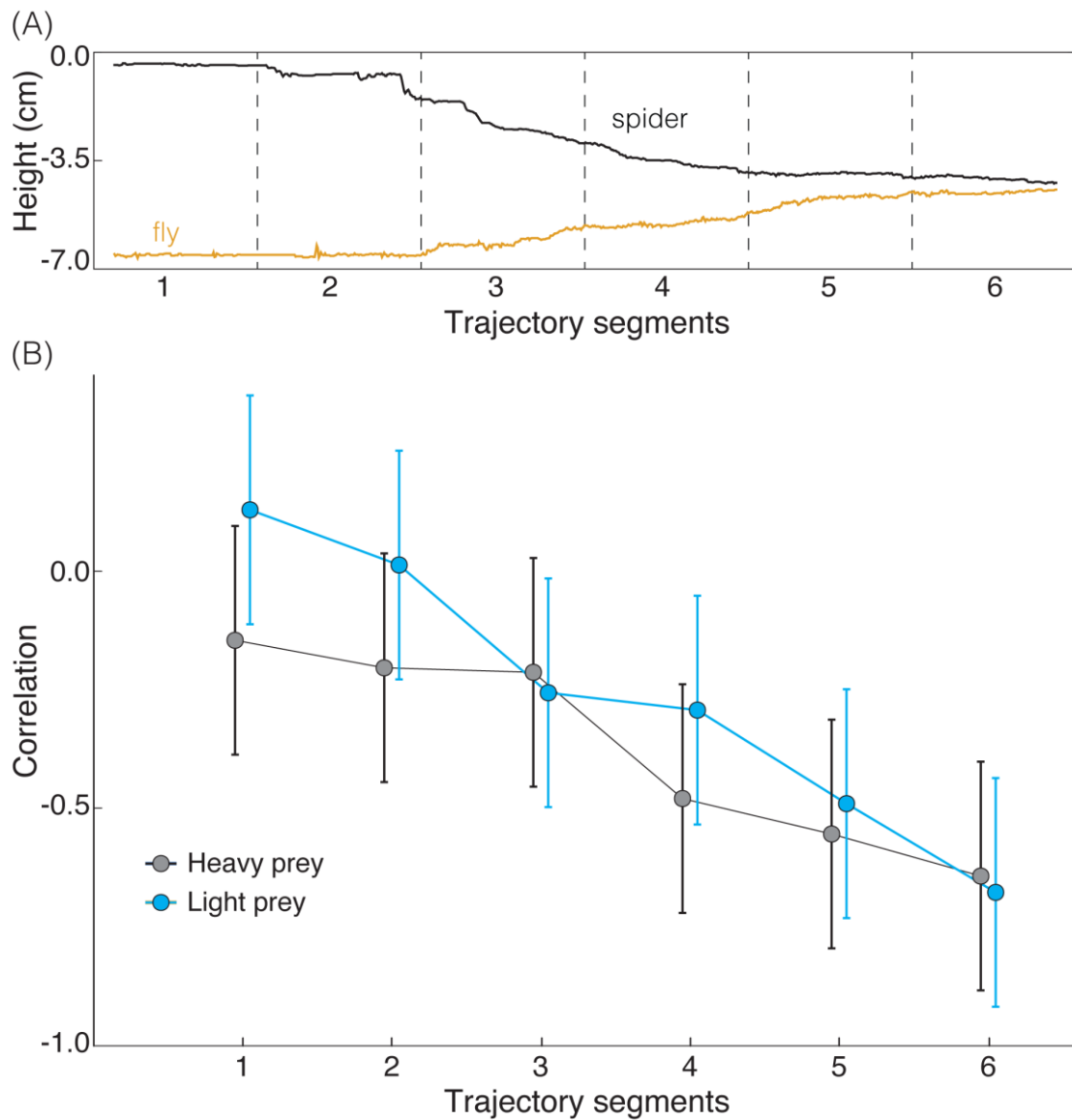
Figure 5: Correlation between spider position and fly position in two treatments (Heavy prey (blue lines) and Light prey (yellow lines)) over six segments of the trajectory. Fig. 5A shows a sample trajectory with demarcation of segments. In Fig. 5B, note that as the trajectory progresses, the correlation in spider and fly positions are increasingly negatively correlated, implying that as the spider is lower in the web, and the fly is higher, as a result of reeling behaviour.
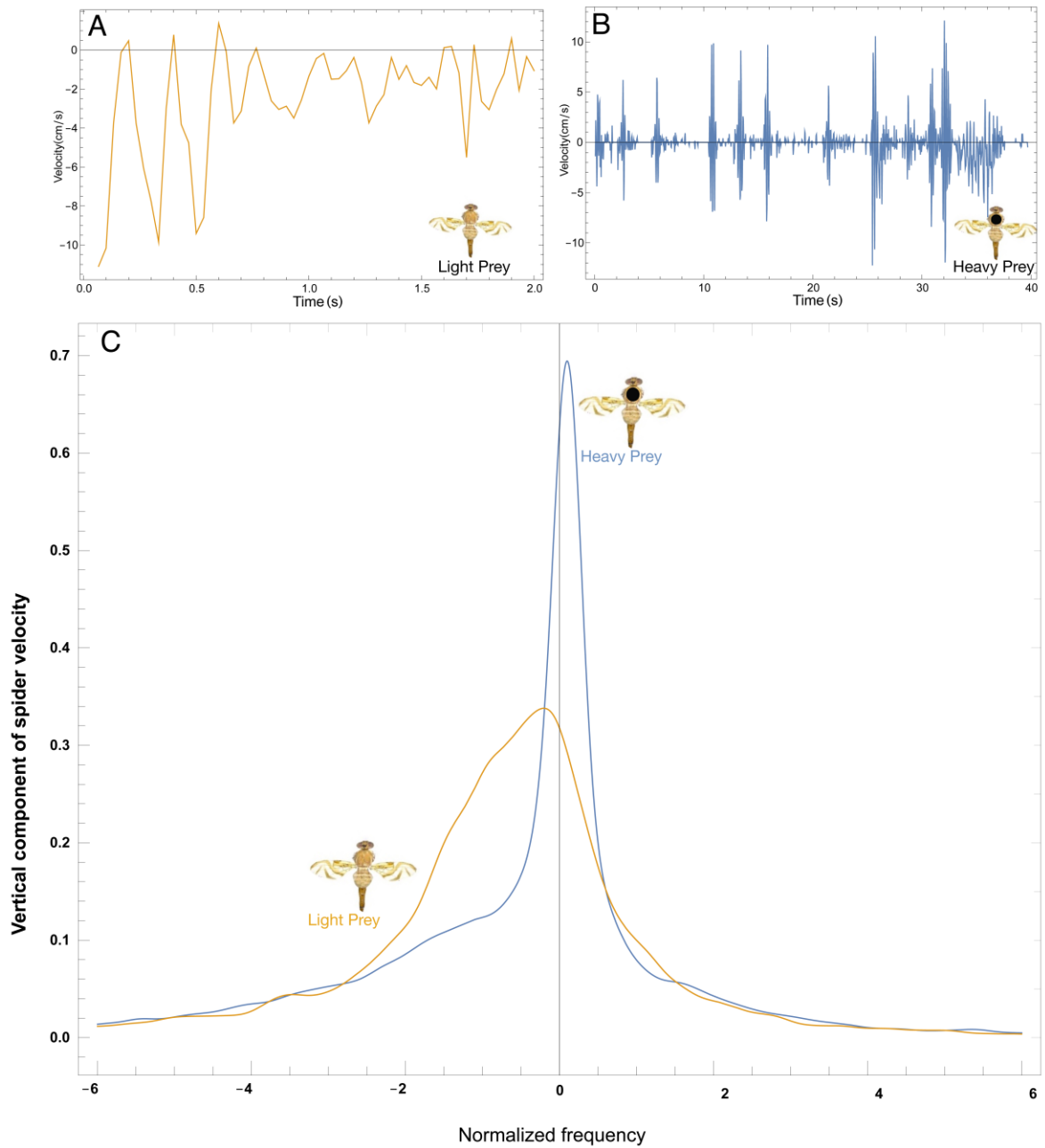
Figure 6: Sample velocity profiles of spiders approaching Light prey (A) and Heavy prey (B) on the vertical axis. Negative values represent spiders going downwards on their way to the prey, and positive values represent an upward motion. When the spider's velocity is zero, it indicates that the spider is momentarily at rest during a change in velocity. We plotted the frequencies of velocity state

change for all spiders in C. Note that in both heavy and light treatments, there is a

peak at zero but the peak is significantly higher for the heavy treatment suggesting

that there is more fluctuation in velocities in spiders approaching heavy prey.
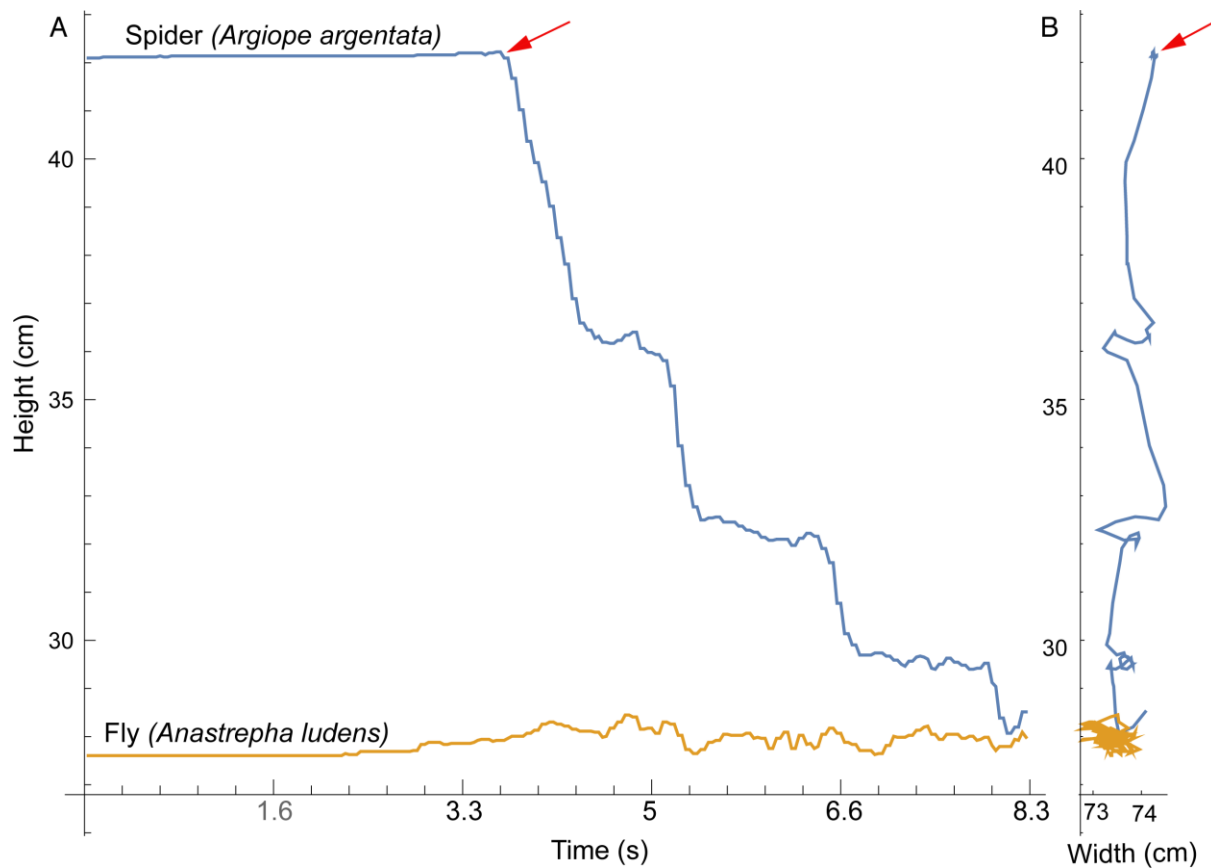
Figure 7: A. A sample trajectory of an *Argiope argentata* spider (blue line) as it approached the prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis represents the time taken for the spider to make contact with the fly. The red arrow shows the start of the spider's run to the prey. B. A sample trajectory of the prey capture sequence seen with both X and Y components of the trajectory.

TABLES

Table 1: Summary of experiments and tests conducted in the study

Experiments			Tests
Description of reeling	Non-manipulated flies	1	-
Experiment 1: Characterisation of the behaviour	Non-manipulated flies	29	Summary stats
Experiment 2: Trajectory and velocity analyses	Heavy flies/Light flies	14/13	Unsupervised cluster analysis/ Velocity profiles

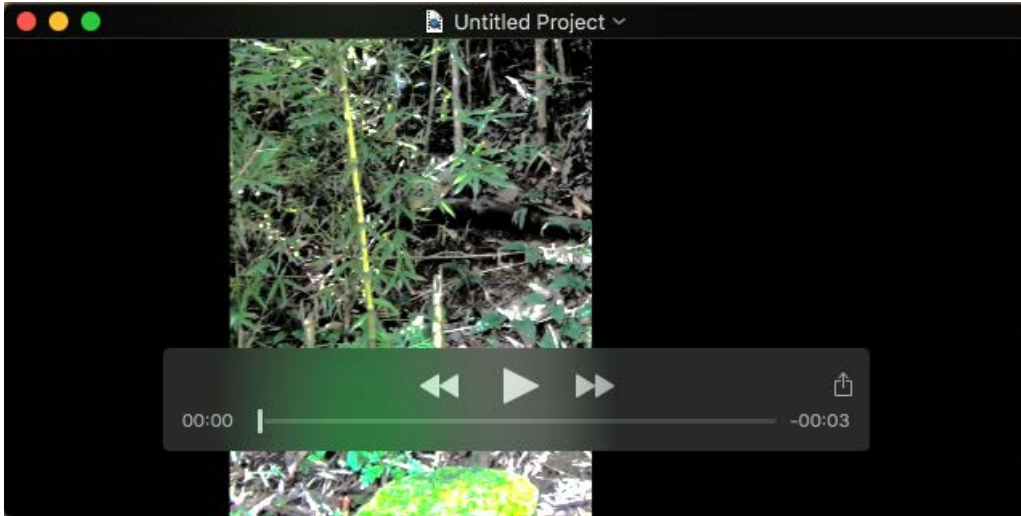Table 1: Summary of experiments and tests conducted in the study

Table 2: Summary statistics for the analysis of correlation between spider position and fly position in two treatments (Heavy prey and Light prey) over six segments of the trajectory.

ANOVA

	Sum of Squares	df	Mean Square	F	p
Model	9.233	11	0.839	4.361	< .001
Treatment	0.476	1	0.476	2.475	0.118
Segment of trajectory	8.169	5	1.634	8.489	< .001
Treatment ✳ Segment of trajectory	0.588	5	0.118	0.611	0.692
Residuals	27.713	144	0.192		

Note. R-squared= 0.25 , adjusted R-squared= 0.193

Supplementary Files

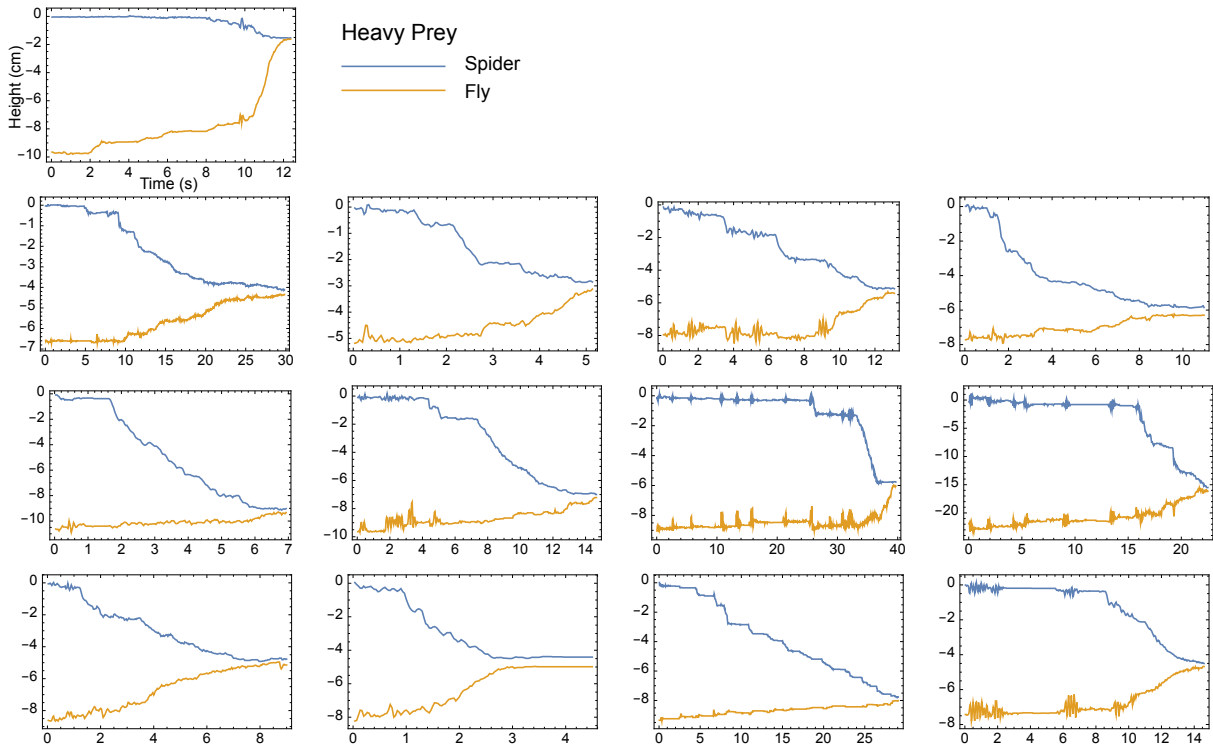Movie 1. Movie showing the reeling behaviour in *Verrucosa arenata*.

Figure S1: All trajectories of *V. arenata* spiders (blue line) as they approached Heavy prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis is the time taken (in seconds) for the spider to make contact with the fly.
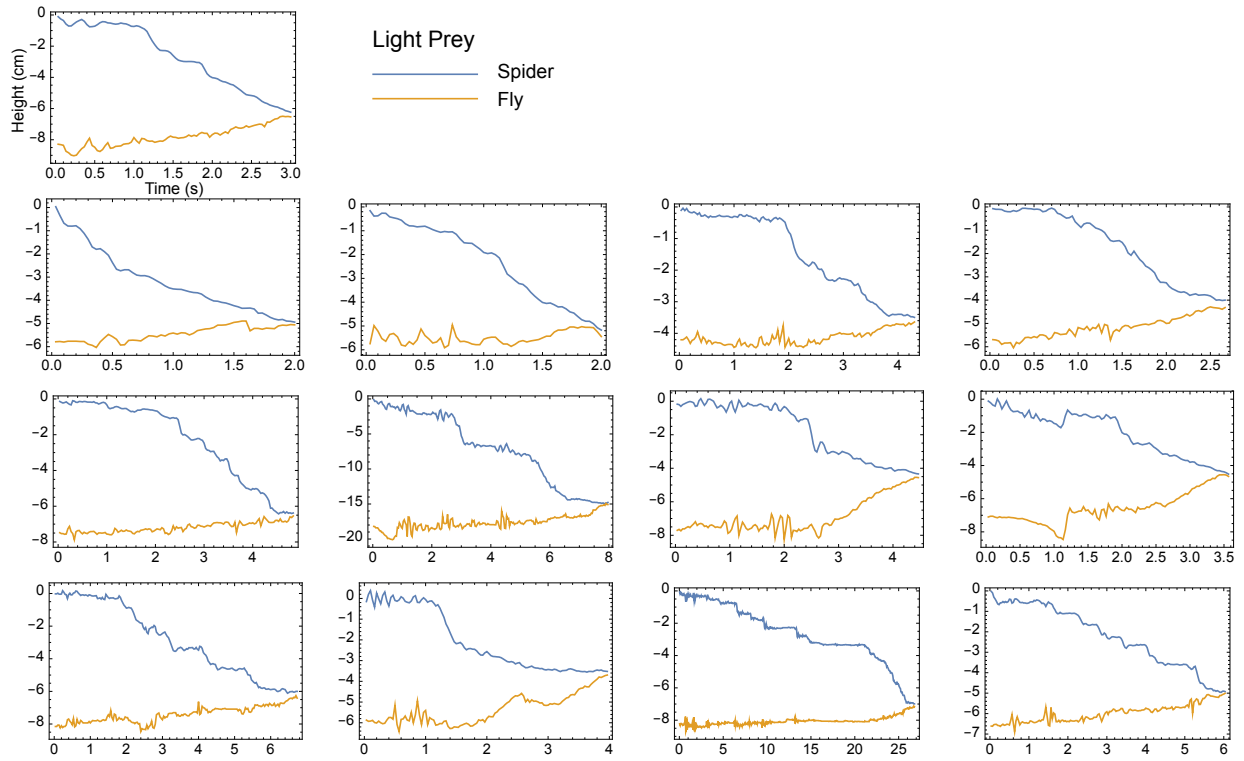
Figure S2: All trajectories of *V. arenata* spiders (blue line) as they approached Light prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis is the time taken (in seconds) for the spider to make contact with the fly.

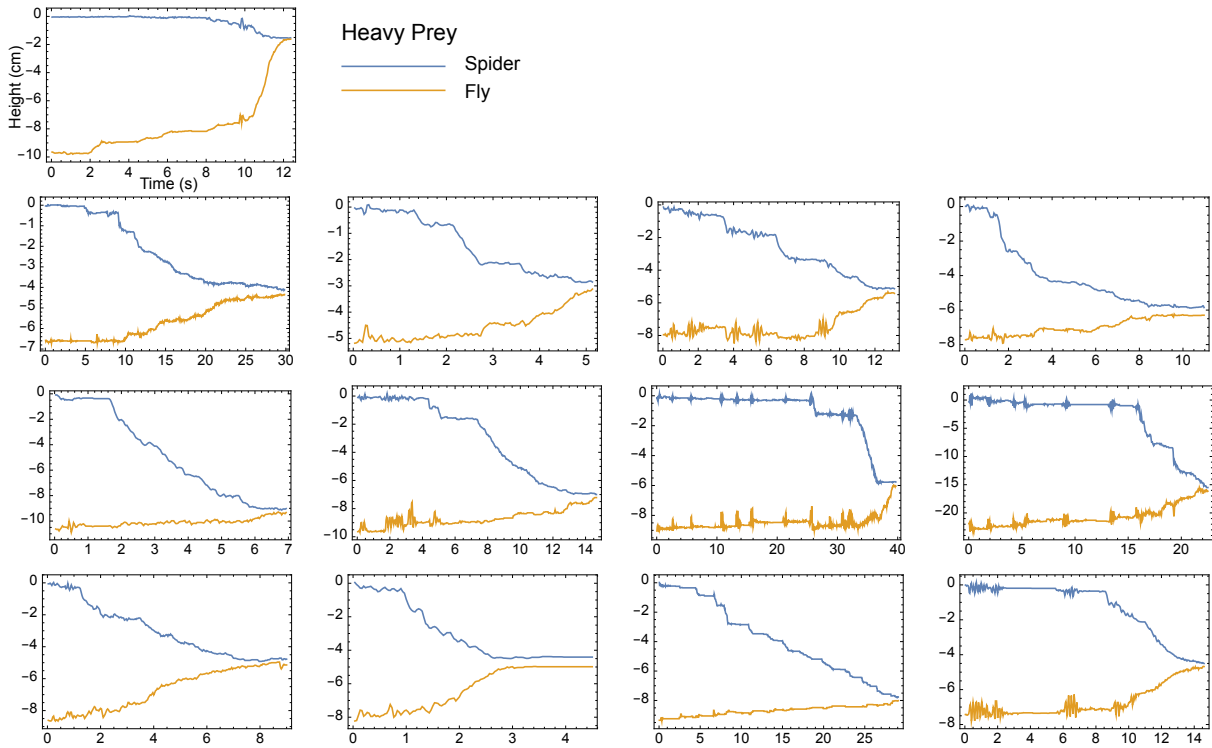Movie 1. Movie showing the reeling behaviour in *Verrucosa arenata*.

Figure S1: All trajectories of *V. arenata* spiders (blue line) as they approached Heavy prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis is the time taken (in seconds) for the spider to make contact with the fly.
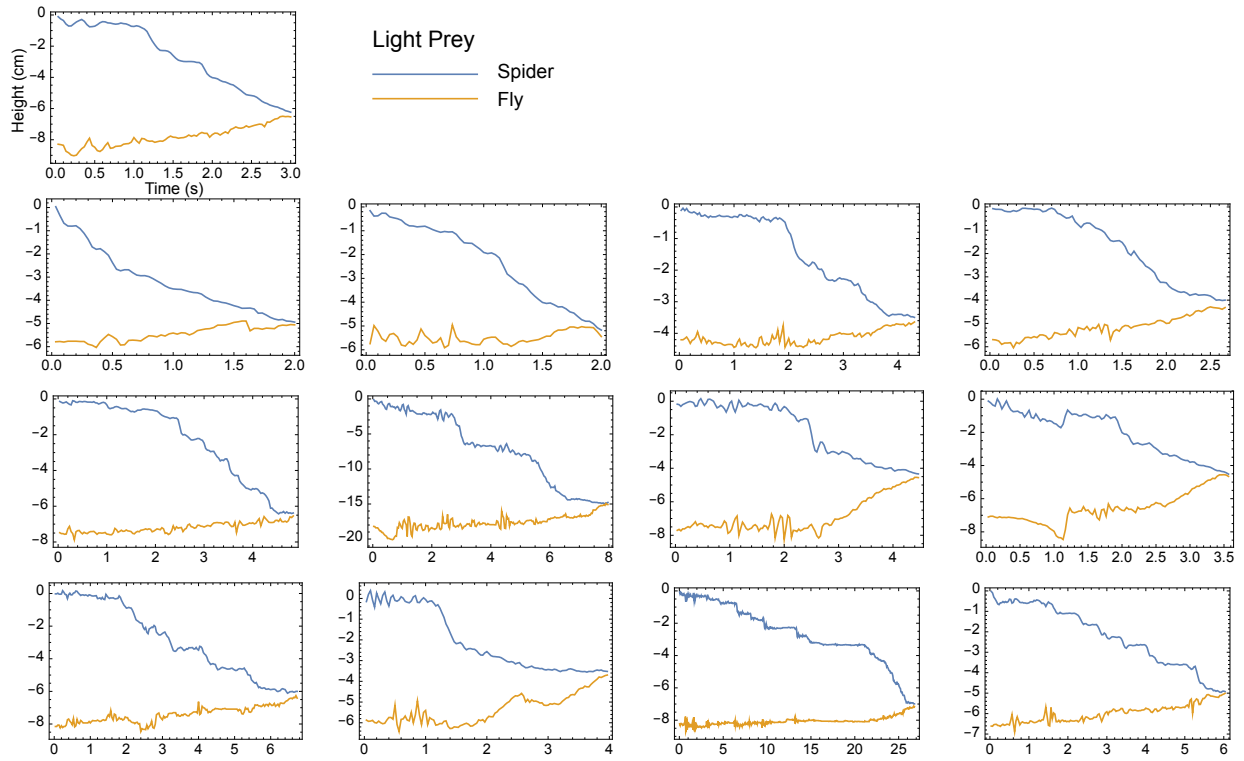
Figure S2: All trajectories of *V. arenata* spiders (blue line) as they approached Light prey (*A. ludens*; yellow line)), shown here as a time series plot. The Y axis represents the vertical component of positions of the spider and fly (i.e., height in the web), and the X axis is the time taken (in seconds) for the spider to make contact with the fly.