

SHORT COMMUNICATION

Functional flexibility in a spider's orb web

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ABSTRACT

Web spiders rely on vibrations propagated via their web to identify, locate and capture entangled prey. Here, we experimentally tested the robustness of the orb weaver's predation strategy when webs are severely distorted and silk tensions are drastically altered throughout the web, a common occurrence in the wild. We assessed prey identification efficiency by comparing the spider's initial reaction times towards a fruit fly trapped in the web, we measured location efficiency by comparing times and number of tugging bouts performed, and we determined capture efficiency by comparing capture times. It emerged that spiders are capable of identifying, locating and capturing prey in distorted webs, albeit taking somewhat longer to do so.

KEY WORDS: Vibrations, Biotremology, Garden spider, *Araneus diadematus*, Predation, Morphological computing, Predator–prey

INTRODUCTION

Studies of animal communication using substrate vibrations (known as biotremology) are beginning to uncover interesting and important features associated with this form of information transfer. It appears that vibration sensing is far from the exception and is common in both invertebrate and vertebrate animal taxa (Hill et al., 2019; Cividini and Montesanto, 2020). Surprisingly, using substrate vibrations for information gathering and for communication works rather well even when the substrate is highly heterogeneous (Hill and Wessel, 2016; Mortimer et al., 2018a). This observation is not trivial because key characteristics of vibration propagation are linked to the material properties of substrates (Mortimer et al., 2016, 2018a,b; Mortimer, 2017; Hill et al., 2019; Oberst et al., 2019; Cividini and Montesanto, 2020), which suggests that animals that use substrate-bound information are able to correctly interpret signals that could be severely modified in transit.

Orb weaver spiders and their webs are of special interest in this context (Vollrath, 1979; Barth and Geethabali, 1982; Klärner and Barth, 1982; Barth, 1985; 1986; Watanabe, 2000; Foelix, 2010; Witt and Rovner, 2014; Mortimer et al., 2014, 2016, 2018b; Mortimer, 2019). Orb webs are efficient prey traps with many features optimised for the interception and retention of prey and their localisation by the spider (Uetz et al., 1978; Rhisiart and Vollrath, 1994; Vollrath et al., 1997; Schneider and Vollrath, 1998;

Herberstein et al., 2000; Nyffeler, 2009; Wu et al., 2013; Burtscheidt et al., 2019; Han et al., 2019). The process of capture seems to rely entirely on web-borne vibrations and spiders carefully tune their webs to manipulate the propagation of such vibrations (Klärner and Barth, 1982; Vollrath, 1992; Wirth and Barth, 1992; Landolfi and Barth, 1996; Watanabe, 2000; Mortimer et al., 2016). Given the adaptability of the various silks involved, spiders have ample options to adjust their webs during construction, including self-tuning by key silks through interactions with environmental conditions such as relative humidity (Rhisiart and Vollrath, 1994; Vollrath et al., 1997; Vollrath, 1999). Importantly, in the wild (as opposed to the lab), spiders are faced with often highly unstable environmental conditions affecting their webs. Windy conditions, for example, can cause spiders to change their webs during construction (Vollrath et al., 1997; Wu et al., 2013; Tew and Hesselberg, 2017), but also distort webs after the structure has been completed (Movie 1). Because the propagation of vibrations is affected by silk tension (Eberhard, 1981; Barth and Geethabali, 1982; Barth, 1985; Mortimer et al., 2014, 2016), it stands to reason that post-construction web distortion impacts the efficiency with which spiders use vibrations for prey capture. Crucially, Turner et al. (2011) found that prey capture times increased in windy conditions and thereby demonstrated that minimising capture times is important for spiders.

The present study aimed to examine the efficiency with which orb spiders identify, locate and capture prey in webs that are distorted post-construction to mimic, in a controlled way, the effects of environmental distortion. We specifically selected a shearing deformation to distort the webs, as webs are commonly anchored to environmental structures that move independently of each other when disturbed by wind. Notably, our experiment did not set out to test small distortions but instead investigated what happens when viscoelastic self-tuning is overwhelmed at large distortions applied unevenly across radials. We therefore hypothesised that the distortion of webs would decrease the efficiency of prey identification, location and capture compared with non-distorted control webs.


MATERIALS AND METHODS

Spider and prey preparation

Female garden cross spiders (*Araneus diadematus* Clerck 1758) were collected in Oxfordshire, UK. The spiders were housed in our standard Perspex frames (30 cm×30 cm×5 cm) separated by greased Perspex sheets. Unless stated otherwise, twice a week spiders were spray-watered and fed two dead *Drosophila melanogaster*. Spiders from the population were selected at random and transferred into individual flexible frames that were identical to our standard frames except for the corners being flexible. During the preparation period, spiders were required to build two trial webs in the experimental frames and were fed a dead female *D. melanogaster* after each build – female flies being identified by their larger size according to Mathews et al. (2017). After feeding the spiders, the webs were watered and all radials were

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broken except one radial north and south of the hub. Individuals that constructed webs on two consecutive days were subsequently used for experiments.

For the experiments, live female *D. melanogaster* were caught from a stock population in individual Eppendorf tubes and placed on ice for 30 s immediately prior to the actual experiment. This ensured they were motionless when placed in the web but regained mobility when warming up to room temperature. Flies were handled by the wing with tweezers and dipped in water to improve adherence (Sahni et al., 2010), and frames were tapped by hand to ensure spiders did not notice prey placement.

Experimental procedure

The flexibility of the frame allowed us to shear a web from the control into the treatment position with the result that tensions in the web were visibly distorted (Fig. 1A,B). Tension changes were not characterised directly because it was impossible to measure tension in individual radials without damaging the web prior to the experiment.

Over a 4 day experimentation period, we aimed to record 8 videos per spider, i.e. one control run and one treatment run per day. The effect of tension history due to run order (1st or 2nd on a given day) was statistically controlled (outlined below) and tension history was deleted between days as spiders built new webs. After a flexible frame was positioned on the distorter for the first run of the day, spiders were allowed to settle for 5 min before a motionless prey was placed in the web. Prey were placed east and west of the hub because the vertical symmetry in webs should cause tension changes to be approximately equal (Fig. 1B). We note that prey placement in the web corners may test for more extreme distortions while our approach tests for average distortions. Moreover, prey placement east and west of the hub rather than in the corners removes the effect of prey location on travel times as the travel speeds east and west are equal and fall between those in the upward (slower) and downward (faster) direction (Rhisiart and Vollrath, 1994). Distances between spider and prey were not recorded or actively altered. While distances varied from ~3 to 7 cm between webs, placement distances of the two prey per web were kept as similar as possible.

After the spider captured the first prey, the frame was repositioned from control to treatment or vice versa, and spiders were allowed to re-settle at the hub for 5 min before another prey was placed on the opposite side of the hub for the second run of the day. The 4 day experimentation period enabled us to obtain data for all combinations of frame state (control or treatment), run order (1st or 2nd) and prey position (east or west).

Measurements

All trials were filmed at 180 frames s^{-1} (Panasonic LUMIX GH5 digital camera, and a Nikon AF NIKKOR 50 mm lens). Four measurements were obtained from the resulting videos (5.5 ms resolution) to assess the efficiency with which spiders identified, located and captured prey in control and treatment webs. The spider's reaction time, i.e. the time difference between the prey's first movement and the spider's orientation response towards the prey, allowed us to calculate prey identification efficiency. Prey location efficiency was measured by the effort it took the spider to locate the prey and the time it took; location time is the span between the spider beginning its orientation and starting its dash towards the prey, while we calculated the spider's effort by the number of radial tugging bouts performed. Tugging bouts generally consisted of approximately 2–3 radial tugs in rapid succession that arguably formed one continuous action. Tugging bouts were clearly separated by temporal pauses and were more suitable for counting than single tugs. Lastly, prey capture efficiency was measured by the span between the start of the dash and the spider touching the fly with at least one leg.

Statistical modelling

The response data were analysed with mixed models (Davies and Gray, 2015) to assess the effect of frame state (control versus treatment, Fig. 1A) on each of the four measures. The continuous reaction time, location time and capture time data were analysed with linear mixed models (LMMs) with Gaussian error distribution. These data were log-transformed to attain approximately normal data distribution. Histograms of the log-transformed reaction time (LRT), location time (LLT) and capture time (LCT) data demonstrated sufficient normality for LMM analysis. Counts of

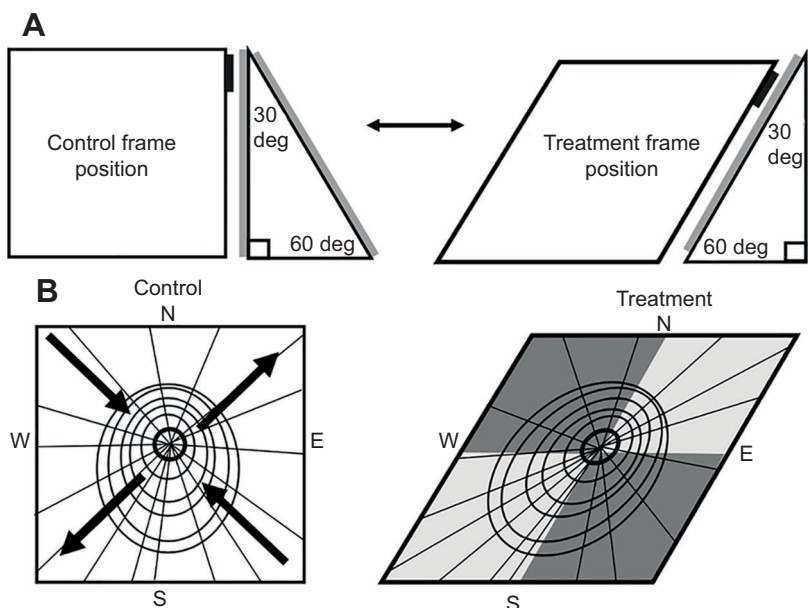


Fig. 1. Orb web distortion treatment and theoretical tension changes. (A) Magnets (black blocks) secured frames to metal strips on the distorter (grey strips). The distorter holds the web squarely (control) or sheared 30 deg to the right (treatment). Webs were repositioned slowly from one static position to the other (over ~30 s) to avoid radial tearing. (B) Shearing a web moved the SE and NW corners closer, and the NE and SW corners further away from the hub (thick central circle) as indicated by the arrows (N, north; E, east; S, south; W, west). In treatment webs, radial tensions in the SE and NW corners were reduced (dark grey shading) whilst radial tensions in the NE and SW corners were increased (light grey shading). See Fig. S1 for a photographed web in a flexible frame in the control and treatment position.

tugging bouts were analysed with a generalised linear mixed model (GLMM) with Poisson error distribution (Berk and MacDonald, 2008; Thomas, 2017). Poisson GLMMs do not require normally distributed data (Thomas, 2017).

In all models, the frame state (control or treatment) was specified as a fixed effect, and spider ID and run order (1st or 2nd run on a given day) were specified as random effects. Spider ID adjusted for pseudoreplication caused by multiple measurements obtained from one individual, whilst run order controlled for any effects of data collection order and tension history on one day. Day order (days 1–4) and prey position relative to the hub (east or west) were not included in models because they were controlled for experimentally and boxplots did not indicate a significant effect of either variable (Fig. S2). The final models thus examined whether each measurement (a–d) was affected by frame state when adjusted for variation observed due to run order and any natural variation that may exist between individuals.

The LRT, LLT and LCT LMMs were validated by Q–Q plots, histograms and Shapiro–Wilk tests, which demonstrated that the residuals were normally distributed ($W=0.98$, $P=0.53$; $W=0.98$, $P=0.50$; $W=0.96$, $P=0.13$, respectively). The final LLT and LCT models were overfitted when including both random effects (spider ID and run order). Overfitting occurs when a model is not optimally parsimonious (Hawkins, 2004). However, the random effect variables did not qualitatively affect the outcomes (Table S1). As opted for in previous studies (e.g. Mulder et al., 2020), we elected to accurately represent our experimental design throughout our statistical analysis and retained the random effects in all models despite overfitting. While normality of residuals is not an assumption of Poisson GLMMs, the tugging bout GLMM was assessed for overdispersion, as per the methods in Thomas (2017).

Overdispersion occurs when there is greater variability in the data than predicted by a Poisson GL(M)M (Berk and MacDonald, 2008). No significant overdispersion was found (ratio=1.08, $P=0.33$). The assumptions for all models were met.

RESULTS AND DISCUSSION

All our *A. diadematus* performed the standard actions of orientation, radial tugging and dashing towards the fruit fly; an example of a spider capturing its prey is provided in Movie 2.

Sample sizes

On 51 occasions, spiders successfully identified prey, performed tugging bouts and initiated their dash to prey. However, on one occasion a spider completely stopped before reaching the prey, and on two occasions the fly escaped the web just before the spider reached it. Thus, for reaction times, location times and tugging bouts, the sample size was $n=51$ ($n_{\text{treatment}}=23$, $n_{\text{control}}=28$) and for capture times the sample size was $n=48$ ($n_{\text{treatment}}=21$, $n_{\text{control}}=27$). See Table S2 for the number of runs completed per spider per measurement. Lastly, on two occasions in treatment webs, the spider dashed in slightly the wrong direction along a radial not adjacent to the prey, but this was no reason for exclusion from the data as prey were ultimately captured.

Model results

Reaction times by spiders in control webs and treatment webs did not differ significantly ($n=11$ spiders, d.f.=40.2, $t=0.89$, $P=0.37$; Fig. 2A). However, location times by spiders in treatment webs were significantly longer than in control webs ($n=11$ spiders, d.f.=42.9, $t=2.29$, $P=0.03$; Fig. 2B). The number of tugging bouts performed in treatment webs was likewise significantly higher than in control

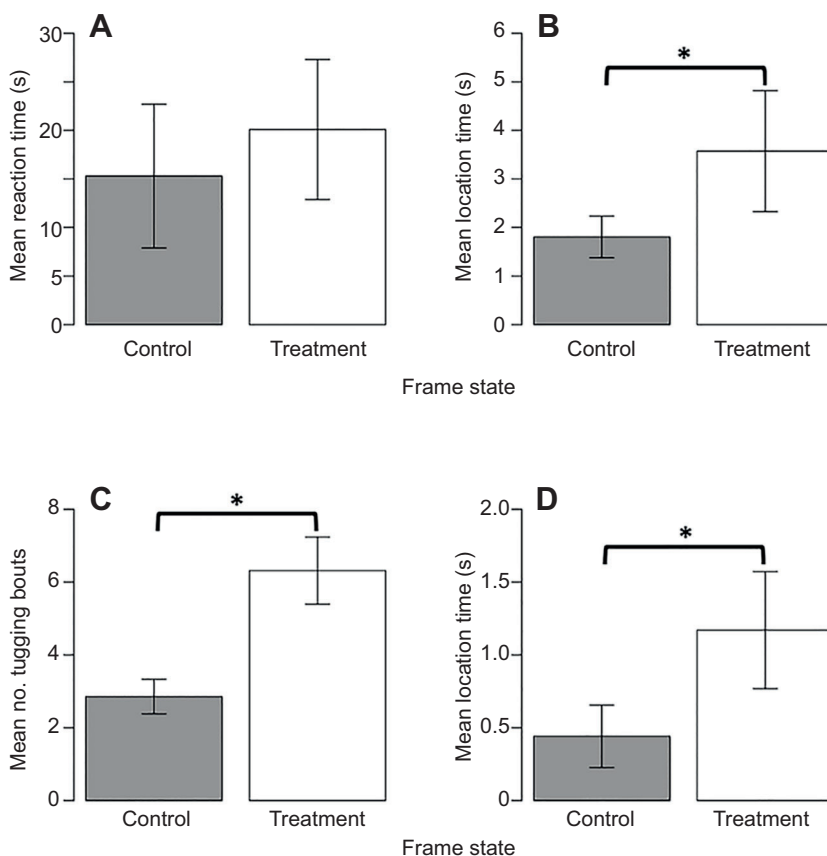


Fig. 2. Orb weaver mean reaction times, location times, number of tugging bouts and capture times in control and sheared treatment webs. (A) Time difference between when the prey first moves and the moment the spider starts its orientation towards the prey. (B) Time difference between when the spider first starts its orientation and the moment the spider starts its dash towards the prey. (C) The number of radial tugging bouts performed by the spider. (D) The time difference between when the spider starts the dash and the moment it reaches the prey with one leg. Plotted values (means \pm s.e.) were calculated from back-transformed (exponentiated) model outputs. $n=11$ spiders; in A–C: $n_{\text{treatment}}=23$, $n_{\text{control}}=28$; in D: $n_{\text{treatment}}=21$, $n_{\text{control}}=27$. *Significant difference ($P<0.05$).

webs ($n=11$ spiders, $z=5.83$, $P<0.005$; Fig. 2C). Lastly, capture times were significantly longer in treatment webs than in control webs ($n=11$ spiders, $t=3.30$, $P<0.005$; Fig. 2D).

These results partly reject our hypothesis; spiders identified prey equally quickly in both web types but took longer to locate prey, performed more radial tugs and took longer to reach prey in distorted treatment webs (Fig. 2). We note that spider web silks under higher tension have increased speed and amplitude of both transverse and longitudinal waves (Frohlich and Buskirk, 1982; Mortimer et al., 2014, 2016). Our treatment altered the tension (Fig. 1B) and therefore changed the propagation speed and relative amplitude of waves in different radials, with minimal effect on the frequency of propagating waves (Mortimer et al., 2014).

Our observations suggest the following. The time it takes a spider to identify a prey depends on (i) the propagation speed of vibrations through the web and (ii) the processing speed of the spider, with identification happening at some threshold value that combines both frequency and amplitude of a vibration (Klärner and Barth, 1982). Our treatment was unlikely to affect reaction times (Fig. 2A) as the effect of changed tensions on propagation speed was probably below this threshold, i.e. too small to make a difference to the spider's sensory perception (Mortimer et al., 2018b). Such sensory thresholds probably differ between species, as another spider (*Octonoba sybotides*) responds more quickly to small prey in webs with increased tensions (Watanabe, 2000).

We may assume that the spider orientates towards a prey by (i) comparing the difference in longitudinal wave amplitude perceived via different radials and (ii) estimating the distance to a prey from the ratio of peak transverse wave amplitudes perceived via different radials (Landolfa and Barth, 1996; Mortimer et al., 2018b; 2019; Mortimer, 2019). Our treatment would have directly compromised these inter-radial amplitude comparisons for orientation and distance estimation, leading to increased location times (Fig. 2B).

Positional information from radial tugging is likely to come from 'vibratory echoes' and standing waves caused by entangled prey (Wirth and Barth, 1992; Landolfa and Barth, 1996; Mortimer et al., 2014). Distorted frequencies and echoes in treatment webs would affect the information gathered by a tugging bout, requiring more bouts to pinpoint the prey's location (Fig. 2C). Performing additional bouts takes extra time, which would have added further to location times (Fig. 2B).

Spiders generally approached prey by climbing along radials directly adjacent to the prey. Altered radial tensions may simply have made it more difficult for spiders to climb to prey and thus increased capture times (Fig. 2C). Alternatively, spiders in treatment webs may also have performed more small tugs on their way to prey, which would slow the speed of travel. It could be argued, and investigated in a field study, that spiders may target prey preferentially in moments when a web is not distorted (in the wild by a gust of wind) in order to shorten travel time to optimise prey capture efficiency while at the same time minimising their own risk of predation by a bird.

To conclude, our semi-natural environment where webs were not fixed in position but were distorted regularly, negatively affects both prey location and subduction. However, this effect was rather small, considering the major distortion of the tension landscape that is considered so important for a haptic spider. This is not really surprising in a unit (spider and web) that has evolved over millennia, in a life-dinner arms race with its prey in a natural environment that contains contorting variables like wind and swaying anchor lines. However that might be, our study suggests that further examination of spider webs in the wild might be necessary to better understand

the orb web's fundamental function as a platform for information transfer. We predict that comprehensive distortion-based biotremology research of spider webs and other study systems is likely to demonstrate that the use of substrate vibrations for information transfer is much more sophisticated than initially thought. Outcomes will have implications not only for our understanding of vibration-dependent animal behaviour but also for engineers developing bioinspired vibration sensors.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.M., F.V.; Methodology: T.M., B.M., F.V.; Validation: B.M., F.V.; Formal analysis: T.M.; Investigation: T.M.; Resources: F.V.; Writing - original draft: T.M., B.M., F.V.; Writing - review & editing: T.M., B.M., F.V.; Visualization: T.M.; Supervision: B.M., F.V.; Project administration: F.V.; Funding acquisition: F.V.

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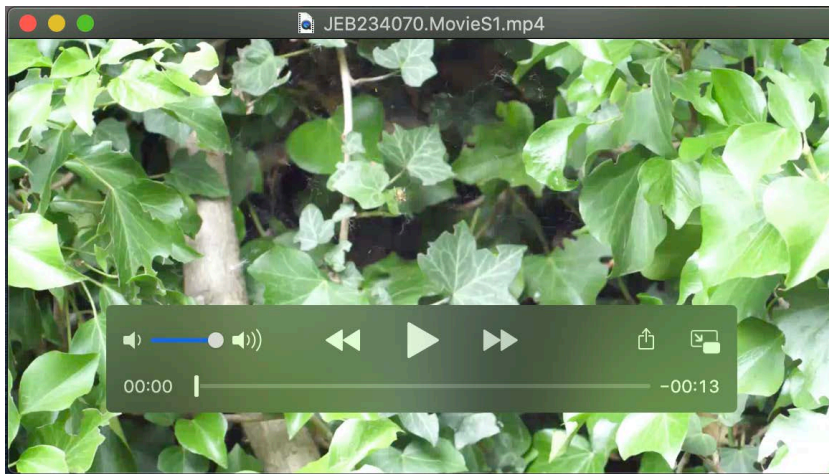
Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.234070.supplemental>

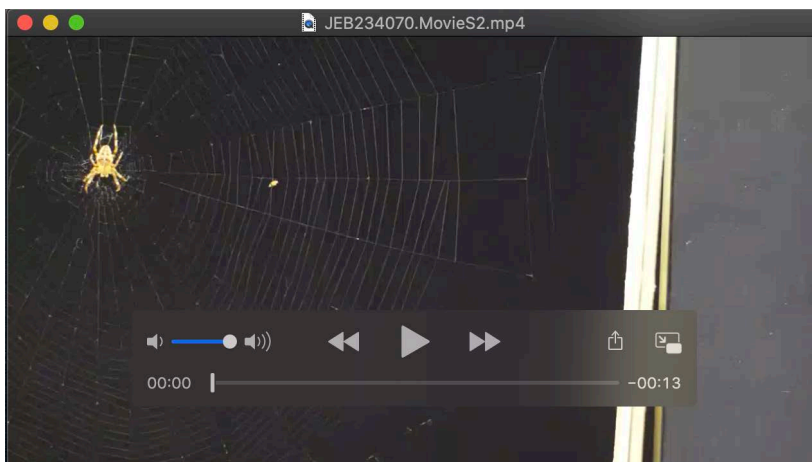
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Movie 1. Wind-induced deformation of an *A. diadematus* web in nature. Video captured at 180fps.



Movie 2. Example prey capture in a control web. Video captured at 180fps.

Fig. S1. An *A. diadematus* web in a flexible frame positioned in the control (a) and treatment (b) position.

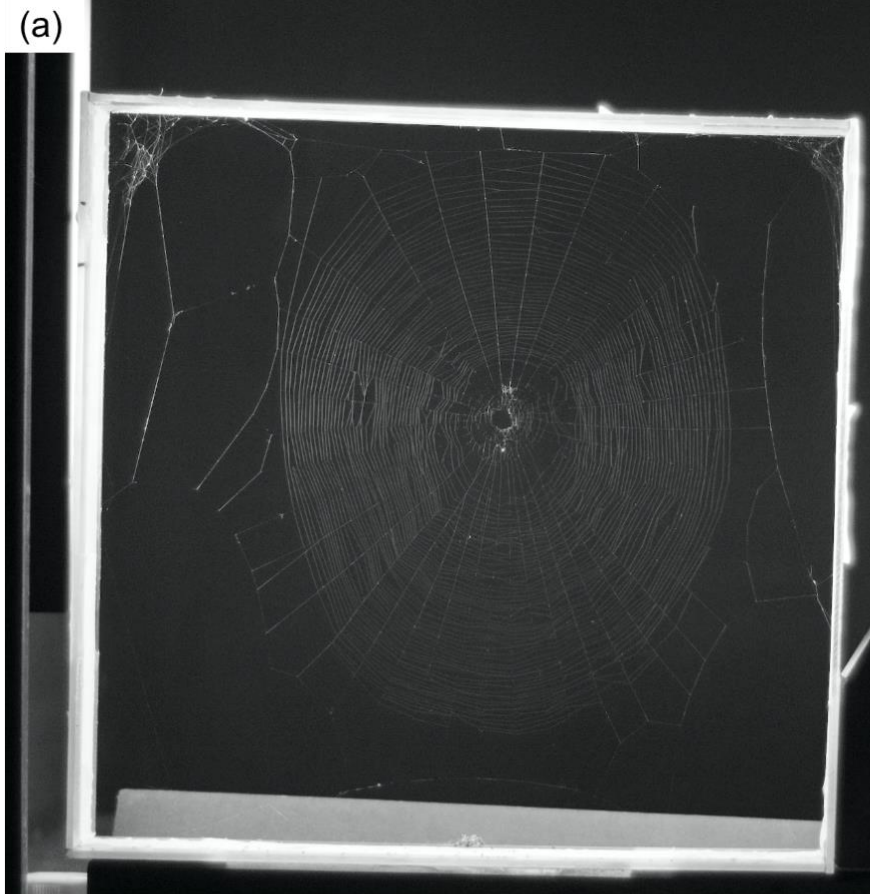


Fig. S2. Box plots demonstrating the lack of an apparent effect of prey position relative to the hub (a), and lack of an apparent effect of experiment order (b), on each of the 4 measures.

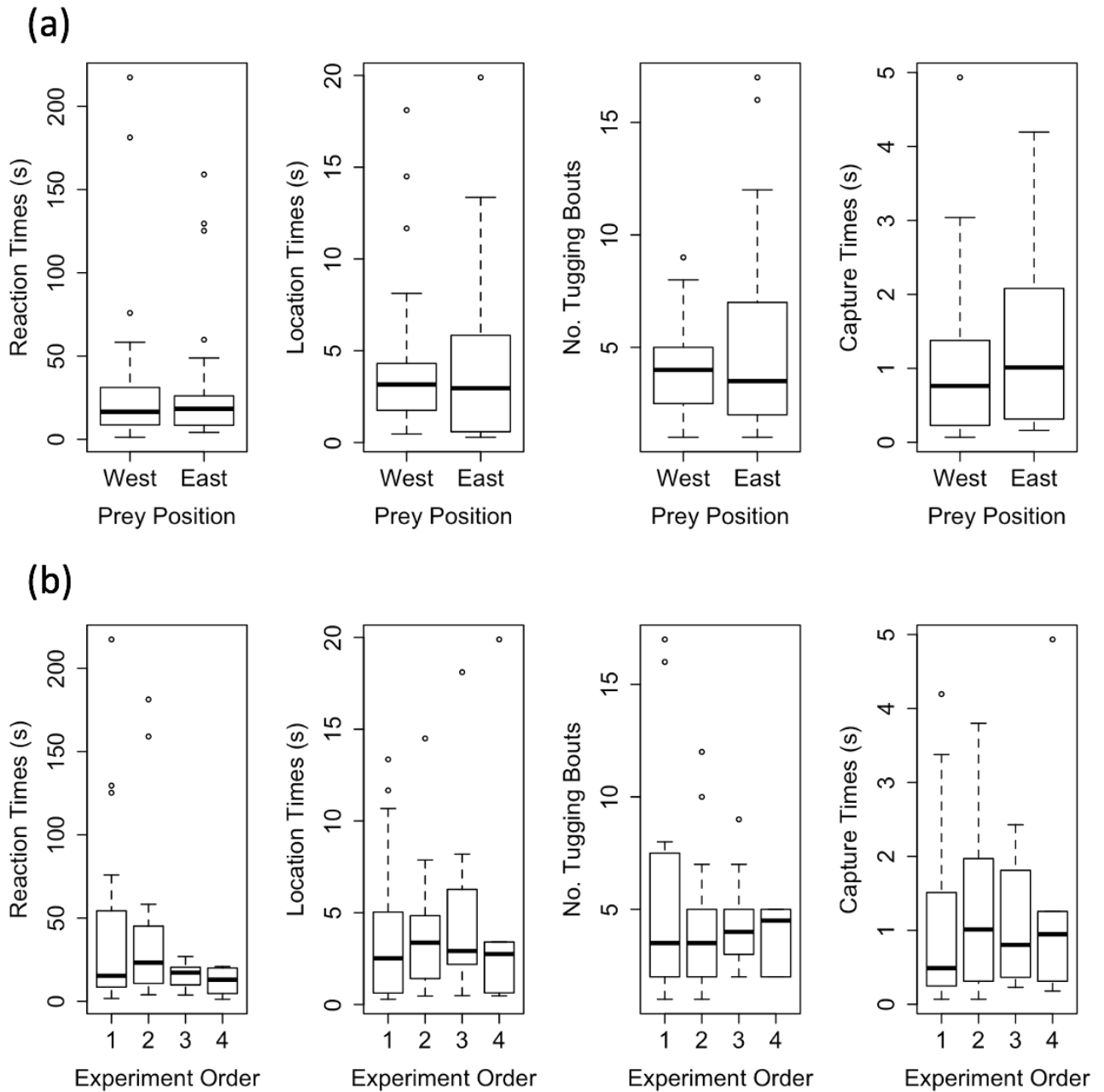


Table S1. Effect of web shearing on log-transformed Location Times (LLT) and Capture Times (LCT) obtained from the models without and with random effect variables.

Fixed effect variable	Effect \pm 1SE (<i>P</i> -value), models 1*	Effect \pm 1SE (<i>P</i> -value), models 2**
LLT		
Control	ref	ref
Treatment	0.66 \pm 0.30 (<i>P</i> = 0.04)	0.68 \pm 0.30 (<i>P</i> = 0.30)
LCT		
Control	ref	ref
Treatment	0.92 \pm 0.31 (<i>P</i> = 0.005)	0.97 \pm 0.30 (<i>P</i> = 0.002)

SE = Standard Error, ref = reference group. *Models 1: Models including the frame state fixed factor**Models 2: Models including frame state as a fixed effect factor in addition to spider ID and run order fitted as random effects. Effect sizes were not back transformed as this was redundant for the required qualitative model comparisons.

Table S2. Samples contributed by each of the 11 spiders to measures a-d.

Spider ID	<i>n</i>	
	RT, LT, TB	CT
174	3	3
177	6	5
178	7	7
181	7	7
189	4	3
193	7	6
194	4	4
196	2	2
199	5	5
201	4	4
202	2	2

RT = Reaction Time (a), LT = Location Time (b), TB = Tugging Bouts (c), CT = Capture Time (d). Spider ID numbers refer to specific spiders in the Oxford Silk Group Lab.