

Multiple prey cues induce foraging flexibility in a trap-building predator

Sean J. Blamires^a, Yi-Chi Chao^{b,1}, Chen-Pan Liao^a, I-Min Tso^{a,c,*}

^aDepartment of Life Sciences, Tunghai University

^bAffiliated High School of National Taiwan Normal University

^cCenter for Tropical Ecology and Biodiversity, Tunghai University

ARTICLE INFO

Article history:

Received 19 October 2010

Initial acceptance 6 December 2010

Final acceptance 14 December 2010

Available online 26 February 2011

MS. number: 10-00720R

Keywords:

assessment rule
behavioural flexibility
environmental cue
extended phenotype
foraging strategy
Nephila pilipes
orb web spider
prey handling
prey type
web architecture

Predators must be behaviourally flexible to counter the temporal and spatial stochastic fluctuations and response variability of their prey. To ensure behaviours are adequate across environments, animals must regularly assess environmental cues. Spider orb webs are an example of a flexible foraging trait in a predator, as web architectural components vary in response to exposure to different prey types and prey traits. The cues used by orb web spiders to initiate changes in web architecture are not known. Current research predicts that prey nutrients and vibratory stimuli are potential candidates, but how they combine to affect spider foraging decisions is not clear. We performed experiments exposing the giant wood spider, *Nephila pilipes*, to different prey nutrients and vibratory stimuli. Spiders were fed either large profitable prey with high kinetic energy (crickets) or small prey with low kinetic energy (flies). In two treatments the prey nutrients and vibratory cues came from live prey, but in the other two treatments spiders received dead crickets with webs stimulated by flies and vice versa. The spiders fed on live flies built larger webs with more radii that were less stiff and had greater vibration damping. These web characteristics did not differ between the other three treatment groups. Our results show that in the absence of nutrient and vibratory cues from profitable prey, spiders alter their web architecture to build webs better able to capture the less profitable prey at a cost of more material investment, greater web visibility and reduced vibratory signal clarity.

© 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

As prey availabilities can vary stochastically and their behaviours vary spatially and temporally, predators often exhibit behavioural flexibility (Krebs & Davies 1987; Bell 1990; Toft & Wise 1999). For example, seasonal changes in prey composition and abundance may expose predators to varying densities of nutritionally profitable and unprofitable prey. Foraging models predict that a predator should aim to capture the most profitable prey in the environment unless this prey becomes rare, in which case it should switch strategy and target the more abundant but less profitable prey (Krebs & Davies 1987). Inappropriate behavioural switching, however, may be costly to a predator (Blumstein & Bouskila 1996). Decisions about behavioural alterations are thus made upon careful evaluation of cues from the environment and are bound by 'assessment rules' (Blumstein & Bouskila 1996). Although there is much documentation of predators exhibiting behavioural flexibility (reviewed by Bell 1990; Heiling & Herberstein 2000), documentation of predators using environmental cues to evaluate the type and profitability of

prey in the environment is limited (but see Page & Ryan 2005; Hansen et al. 2010).

Orb web spiders respond to varying environmental conditions by altering the architecture of their webs (Sherman 1994; Heiling & Herberstein 2000). An orb web is thus depicted as being a flexible foraging tool of an orb web spider, representing a well-documented example of a predator altering foraging behaviour in response to changes in its prey. An orb web, however, is also used for moulting, avoiding predators, regulating water intake, thermoregulation and receiving diverse sensory stimuli via vibrations in the radial threads (Foelix 1996). Therefore, it may be more accurately described as a flexible extended phenotype, depicting the spider's foraging strategy, developmental status, experience and physiological condition (Craig 2003).

As the architecture of the orb web is a product of multiple components (i.e. a frame with attached radial threads, sticky spirals, a hub, a free sector and, in some species, decorations or stabilimenta; Foelix 1996), architectural alterations are made upon complex cost–benefit consideration. The costs include the risks of exposure to predators during web building and occupancy and energetic costs of movement. As some silks are more expensive to synthesize than others (Craig 2003), the various components of the orb web have different costs and, consequently, respond differently to

* Correspondence: I.-M. Tso, Department of Life Science, Tunghai University, No. 181 Section 3, Taichung-kan Road, Taichung City, Taiwan 407-04, ROC.

E-mail address: spider@thu.edu.tw (I.-M. Tso).

¹ Yi-Chi Chao is now at the Department of Dentistry, National Taiwan University, Taipei 100, Taiwan, ROC.

environmental variation (Blamires 2010). In addition, each orb web component has distinct functions and construction costs. The radial threads, for example, propagate vibrations, which provide the spider information about the environment such as the presence of predators or prey, and wind speed (Masters et al. 1986; Landolfa & Barth 1996; Nakata 2008). When more spiral threads are included in an orb web the signal propagated becomes damped (Landolfa & Barth 1996). Spiders may overcome this by investing in more radii or adjusting the tension of the existing radii (Nakata 2010). The number of and/or tension in radial threads may thus be coupled with spiral thread investment. Such parameter covariation is notable in spiders of the genus *Nephila*, as they have particularly narrow gaps between spiral threads (mesh height) relative to the area of their webs (Eberhard 1986; Landolfa & Barth 1996; Tso et al. 2007).

Previous studies have found that feeding frequency, prey size, abundance and handling time affect the architecture of orb webs (Sherman 1994; Herberstein et al. 2000; Venner et al. 2000; Nakata 2008; Blamires 2010). Nevertheless, no study has evaluated whether any of these factors act directly as cues, or are correlated with other factors that act as cues. Orb web spiders alter web architecture when exposed to a single prey type varying in nutritional value (Blamires et al. 2009; Mayntz et al. 2009; Blamires 2010), and when exposed to different radii-propagated vibratory stimuli (Nakata 2008). Prey nutrients and prey-induced radial vibrations are therefore candidates for directly acting cues.

Nephila pilipes is an example of an orb web spider that changes its web architecture and silk properties when feeding on different prey (e.g. crickets versus flies; Tso et al. 2005, 2007; Blamires et al. 2010). Here we investigated the prey cues used to assess the environment and make decisions about altering their web architecture. To test systematically how spiders use these cues, we separated prey-induced web vibratory stimuli from prey nutrients in four treatments: (1) spiders were fed live flies, so received both fly nutrients and fly-induced web stimulation (FF treatment); (2) spiders were fed live crickets, so received both cricket nutrients and cricket-induced web stimulation (CC treatment); (3) spiders were fed dead flies, but received live cricket-induced web stimulation (FD treatment); and (4) spiders were fed dead crickets, but received live fly-induced web stimulation (CD treatment). We used crickets or flies as prey because *N. pilipes* changes its web architecture when feeding on these prey (Tso et al. 2005, 2007), and crickets are larger, thus impact the web with more kinetic energy and supply a greater quantity of nutrients. We measured the orb web architectural parameters described by Tso et al. (2007) as well as web stiffness, radial vibration damping and spiral stickiness, as these parameters may also vary with diet (Higgins & Rankin 1999; Higgins et al. 2001; Townley et al. 2006; Opell et al. 2009).

Nephila pilipes builds a web of smaller capture area, with a greater spacing between spirals and more radii when feeding on crickets compared to when feeding on flies (Tso et al. 2007). According to foraging models, if the spiders detect that crickets have become rare they will switch strategy, whereupon they will build a larger web, with a smaller spacing between spirals and fewer radii (Tso et al. 2007; Blamires 2010). Thus, we made the following predictions. (1) If *N. pilipes* use prey-induced vibratory stimuli and not nutrients as the cue, spiders in the FF and CD treatments should build similar webs, as should those in the CC and FD treatments. (2) If nutrients are used as a cue, and not prey-induced vibratory stimuli, then the spiders in the FF and FD treatments should build similar webs, as should those in the CC and CD treatments. (3) If vibratory stimuli and nutrients are used as cues in combination, spiders in the CC, CD and FD treatments (i.e. those with either cricket-induced vibratory stimuli or nutrients) should build different webs to those in the FF treatment (i.e. those with no cricket-induced cues). (4) If neither the prey-induced vibratory stimuli nor nutrients are cues then all of the

webs should differ, as the true cues used would not have been identified in the experiments.

METHODS

Spider Collection and Pretreatment

We collected 60 penultimate-instar female *N. pilipes* (15–20 mm body length) from secondary forests in Taipei County, Taiwan. We measured their body length with digital callipers (accuracy to 0.1 mm) upon capture. Within 24 h of capture, the spiders were taken to an unused room fitted with evenly spaced steel wires to facilitate web building. The room had ample space so that competition for space and cannibalism did not impede the experiment. Room temperature (about 25 °C) and relative humidity (about 30%) were kept constant throughout the experiment and uncovered windows ensured a natural day:night photoperiod.

We pretreated all of the spiders by feeding them one larval mealworm, placed on the lower right corner of the web, daily over 3 days to ensure maximal nutritional uptake and to eliminate any influence of previous foraging experience over web building and silk production (Tso et al. 2005, 2007; Blamires et al. 2010). Spiders that failed to feed ($N = 7$) each day during pretreatment were not used in the subsequent experiments. We randomly assigned each of the remaining 53 spiders to one of four feeding treatment groups: FF (fed live flies), CC (fed live crickets), FD (fed dead flies but their webs were stimulated by live crickets) or CD (fed dead crickets but their webs were stimulated by live flies) on day 4.

Feeding Regimes

We used laboratory-reared house flies, *Musca domestica*, and crickets, *Acheta domestica*, fed dried yeast, vegetable and agar media ad libitum. Independent experiments (Blamires et al. 2009; Blamires 2010) found crickets to contain a higher percentage of protein than flies (60% versus 40%). In addition to higher protein content, the crickets (body mass around 300 mg) used in this study were about five times the size of the flies (mean body mass around 60 mg), so they were regarded as more profitable and as having higher kinetic energy on web impact. Spiders assigned to the CC and FF treatments had their prey nutrients and vibratory cues coupled. Those assigned to the FF group ($N = 14$) were fed five live house flies, while those assigned to the CC group ($N = 13$) were fed one live cricket. Spiders in the CD and FD treatment groups had their prey nutrient and vibratory cues uncoupled. Those assigned to the FD group ($N = 13$) had one live cricket placed on the web, which was removed and replaced by five (to control for biomass) freshly killed (by exposure to carbon dioxide) flies once the spider had responded to the cricket-induced vibratory stimuli but before the spider could capture the cricket. Spiders assigned to the CD group ($N = 13$) had five live flies placed on the web, which were removed and replaced with one (to control for biomass) freshly killed cricket. For the CC and FD groups, crickets were thrown onto webs from 200 mm in order to hit the sticky capture spirals with enough velocity to become entangled and induce vibrations in the radial threads, but not too much velocity to induce an artificially intense vibratory stimulus. For the FF and CD groups, spiders were fed live flies by placing vials of flies 20 mm from the web and allowing one fly at a time out of the vial. Each fly was released as the previous fly was intercepted by the web.

All prey were placed on the lower right corner of the web to ensure that the location of origin did not influence the vibratory signal received by the spider. We fed spiders each time they constructed a new web, discontinuing feeding after seven webs (Tso et al. 2007), ensuring the spiders were fed at frequencies suited to their individual physiological states and willingness to consume and digest

food and build webs (Tso 1999; Tso et al. 2007; Liao et al. 2009; Blamires 2010). We assigned 21 days as the limit before confounding temporal factors would influence the experiment, so one spider that had not built seven webs within 21 days was not included in the analyses. Spiders that refused food upon building a new web ($N = 4$) and spiders that died ($N = 1$) or moulted ($N = 3$) were also not included in analyses. We placed live prey on the web to simulate the vibratory stimulus induced by a fly or cricket, as prey do not constantly stimulate the web but provide pulses of stimuli as they struggle (Parry 1965), and these pulses cannot be precisely replicated using a vibrator. Replacing the live flies and crickets with dead prey did not deter any spider from attacking or consuming the latter. We also did not notice any difference in spider handling behaviours when attacking live crickets or flies as opposed to dead crickets or flies. Removing prey was unlikely to induce vibrations in the web that are recognized as prey by the spider (Barth 1985). We occasionally tore the web when removing the live prey for the CD and FD feeding regimes, but we never observed tears to deter the spiders from attacking the dead prey or to alter web tension; thus tears were unlikely to alter the architecture of successive spider orb webs.

Web Measurements

Web architecture

Each web of every spider was lightly sprayed with water to render it visible. We first counted all the radii from the orb webs. Then the hub, orb radius and sticky spirals in the four cardinal directions (up, to the right, down and to the left) were measured or counted. We counted the radii intercepting the outermost spiral, starting at the top of the orb. We found, as did Tso et al. (2007), that *N. pilipes* had few split radii (less than one in every 30 radii), so this was a reliable measurement (Zschokke 1999). We calculated, accounting for asymmetry, the catching area from the formula (Herberstein & Tso 2000):

$$\left[\frac{1}{2} \pi r_{au}^2 - \frac{1}{2} \pi (Hr_u)^2 \right] + \left[\frac{1}{2} \pi r_{al}^2 - \frac{1}{2} \pi (Hr_l)^2 \right]$$

$$\text{where } r_{au} = \frac{r_u + \frac{d_h}{2}}{2}$$

$$\text{and } r_{al} = \frac{r_l + \frac{d_h}{2}}{2}$$

Mesh size was then estimated by the formula (Herberstein & Tso 2000):

$$\frac{r_u - Hr_u + r_l - Hr_l}{(S_u + S_l - 2)}$$

where r_u is the radius of the upper orb half, r_l is the radius of the lower orb half, d_h is the horizontal orb diameter, Hr_u is the radius of the upper hub half, Hr_l is the radius of the lower hub half, S_u is the number of spirals in the upper half of the orb web and S_l is the number of spirals in the lower half of the orb web. Total radii length was estimated by the formula (Tso 1999):

$$(\bar{x} \text{ Rweb} - \bar{x} \text{ Rhub}) \times \text{no. of radii}$$

Where $\bar{x} \text{ Rweb}$ is mean orb radius, $\bar{x} \text{ Rhub}$ is the mean hub radius (both averaged from four cardinal directions) and no. of radii is the number of orb radii. Total spiral length was estimated by:

$$(\bar{x} \text{ Rweb} + \bar{x} \text{ Rhub}) \times \bar{x} \text{ no. of spirals}$$

Where $\bar{x}$ no. of spirals is the mean number of spirals (capture and auxiliary) averaged from four cardinal directions. To measure radial thread thickness we freed 200 mm sections of radii using burning incense and mounted them onto 20 × 20 mm cardboard frames, carefully burning away any attached spirals, from the left, middle and right sections of the lower half of the orb using incense. The radial threads were coated with gold for 3 min under 7 mA electrical current and viewed and measured under an S-2300, 15 kV Scanning Electronic Microscope.

Web stiffness

Web stiffness, or the ability of the web to resist elastic deformation when force is applied perpendicular to its surface (Askerland 1994), was measured on the sixth web of each spider. To collect orb webs without altering stiffness, a wooden ring (diameter = 300 mm) with cyanoacrylic glue around its perimeter was placed parallel with the plane of the orb web so that the centre of the orb was approximately equal in height to the centre of the ring. We carefully moved the ring towards the orb web until the central portion of the orb was attached. Burning incense was used to free the periphery of the orb web from the ring. We used a microbalance (± 0.1 g) fixed to the movable arm of a dissecting microscope to measure the force needed to lift a single radial thread vertically a height of 30 mm, measured by a ruler placed vertically beside the ring. We first attached a hook to a radial thread at a point approximately 100 mm from the lower margin of the hub. We then turned the wheel of the microscope, gradually raising the microbalance. The radial thread was held at 30 mm and the mass reading on the microbalance was recorded. This reading was transformed to Newtons force by multiplying by 9.8. The measurement was repeated four times on different radial threads from the lower half of the orb web. All radii were extended within the performance limits of dragline silk (approximately 20% length), ensuring that we did not deform other radii. Only the lower orb half was used because *N. pilipes* constructs an asymmetric orb and the radii in the upper half of the orb were too short for measuring stiffness.

Vibratory damping

The seventh web of 20 spiders ($N = 5$ for each treatment group) was used to estimate vibratory damping. Such an estimate was achieved by applying an artificial vibration source on webs then comparing the extent of spiral thread vibrations of both the origin and a distant point. A continuous vibratory signal (frequency = 66 Hz), within the frequency (10–100 Hz) that elicits prey attack responses in spiders (Barth 1985), was generated by touching a radial thread in the lower margin of the web with an electronic vibrator. Motions from the vibrator caused the spirals to vibrate and we compared the amplitude of spiral thread vibrations at the source and 300 mm vertically away from the source (Landolf & Barth 1996). We used two video cameras (TRV 118, Sony, Tokyo, Japan) to record the amplitudes simultaneously. One was placed in front of the source and the other was placed 300 mm above it. At both measurement points we placed a 10 × 1 mm piece of paper as a standard to calibrate the amplitude of spiral thread vibrations. The motion generated by the vibrator would cause the spiral threads to undulate vertically and the amplitude of vibrations was determined from the video footage. Vibration damping was calculated by the formula:

$$[(A_s - A_{300})/A_s] \times 100\%$$

where A_s is the amplitude at the source and A_{300} is the amplitude at 300 mm vertically above the source.

Spiral stickiness

Spiral threads of the seventh web of 20 different spiders ($N = 5$ for each treatment group) were stuck onto 50 × 50 mm cardboard

frames using cyanoacrylic glue. The sticky spirals outside the frames were burnt with incense to free them from the spirals within the frames. We fixed an acrylic ring on the moving arm of a dissecting microscope so that the ring could be moved by turning the adjustment wheels of the microscope. Cardboard frames containing the sticky spirals were horizontally fixed, using masking tape, onto a wooden platform beside the microscope. The acrylic ring was lowered until it touched a strand of spiral silk. The ring was then pulled up at a speed of 17.0 mm/min. The distance pulled before the spiral thread detached from the ring was recorded as a measure of stickiness; the further the distance the stickier the thread was. The test was performed on five spirals per web and mean values were calculated. Because the distances moved by the threads in this procedure are small (10–20 mm) compared to the elastic potential (up to 300% spiral length), it was assumed that the influence of thread elasticity is negligible (Agnarsson & Blackledge 2009; Opell et al. 2009).

Statistical Analyses

Between-treatment web architecture, vibration damping and spiral stickiness comparisons were conducted using measurements made on the seventh web. Web stiffness comparisons were done using measurements of the sixth web. We used the seventh web for the majority of the comparisons for consistency with Tso et al. (2007) and because we were interested in the prey cues used by *N. pilipes* to assess long-term changes in its prey environment. To assess whether any web architectural parameter (capture area, mesh size, number, length and diameter of radii) differed according to our feeding treatments, MANCOVA was used with body length as the covariate. We used MANCOVA rather than ANCOVA for assessment of the web architectural parameters because the web parameters are not independent (Herberstein & Tso 2000). We used ANCOVA to compare the stiffness of the webs across the four feeding treatments, incorporating number and diameter of radii as separate covariates. An ANCOVA test was also used to compare the spiral stickiness of webs across the four treatment groups, with spider body length as the covariate. A further ANCOVA test was used to compare the vibration damping across the four treatment groups, using mesh height as the covariate. Before performing tests we ensured that all data were normally distributed and all slopes were parallel and homogeneous using Kolmogorov–Smirnov and Parallelism tests, respectively. All percentile data were arcsine transformed prior to analysis. Fisher's least significant difference, LSD, post hoc analyses were done when significance was detected by MANCOVA or ANCOVA. All statistical tests were two tailed.

RESULTS

Forty-four *N. pilipes* ($N = 11$ for each treatment group) built seven webs and completed the experiment. The architectural parameters

of the seventh web of spiders in the FF (live flies) treatment had larger capture areas, more and longer radii of similar diameter, and longer spiral threads; therefore FF spiders invested more silk in their webs than spiders in the other treatments (Table 1). Web architectural parameters did not differ significantly between the seventh webs of *N. pilipes* in the CC, FD or CD treatment groups.

The mesh heights of the seventh webs of *N. pilipes* in the FF group were smaller (although not statistically significant) than those of spiders in all other treatments (Table 1). Considering the effects of number of radii and thread thickness, the stiffness of webs differed significantly across the four treatments (Table 2). We found that the webs of spiders in the FF group were significantly less stiff than those of spiders in the other three treatment groups (LSD post hoc analyses: all $P < 0.05$; Fig. 1a).

A preliminary ANCOVA showed that mesh height did not significantly influence vibration damping ($P = 0.538$), so we performed an ANOVA test and found that vibration damping in *N. pilipes* webs differed significantly across the four treatment groups (Table 3), with the radial threads of spiders in the FF group having significantly reduced vibratory signals over 300 mm compared to those of the other treatment groups (Fig. 1b). The rates of vibration damping in the radial threads of spiders from the CC, CD and FD treatment groups were not statistically different (Fig. 1b). Stickiness of the webs built by spiders differed significantly across the four treatment groups (Table 4), with spiders in the CD group having webs of significantly greater spiral stickiness than those of the other three treatment groups (Fig. 1c).

DISCUSSION

We found that *N. pilipes* built webs of greater capture area with more and longer radial threads and longer spiral threads, thus greater silk investment, when feeding on live flies (FF treatment group) than in any other treatment. There was no significant difference in any web architectural parameter, web stiffness or vibration damping between spiders in the CC, FD and CD experiments. This concurs with our prediction that both the prey-induced vibratory stimuli and prey nutrients are used as cues by *N. pilipes* to alter their architectural parameters. Accordingly, if *N. pilipes* are either feeding on crickets or experiencing cricket-induced vibratory stimuli they will build webs aimed at catching crickets.

Crickets are approximately five times heavier and have greater protein content (Blamires et al. 2009; Blamires 2010) so are the more profitable of the two prey items for a spider to consume. Therefore, if optimization of protein intake is the objective of foraging for spiders (Mayntz et al. 2005), our results suggest that *N. pilipes* preferentially forages for crickets (the largest and most profitable prey in its environment), switching to foraging for flies when they ascertain, by a combination of prey-induced vibratory and nutritional cues, that crickets have become rare, consistent with our predictions based on foraging models (Krebs & Davies 1987). We acknowledge, however,

Table 1
Mean $\pm$ SE geometry properties of webs built by *Nephila pilipes* in four treatment groups and results of a MANCOVA test

	Catching area (m ²)	Mesh height (mm)	No. of radii	Spiral length (m)	Total length of radii (m)	Diameter of radii (μ m)
Treatment (main effect)						
CC	31.30 $\pm$ 427 ^a	6.36 $\pm$ 0.46	107.45 $\pm$ 12.27 ^a	20.10 $\pm$ 289 ^a	27.27 $\pm$ 488 ^a	3.95 $\pm$ 0.16
FF	45.84 $\pm$ 342 ^b	5.06 $\pm$ 0.39	154.55 $\pm$ 9.96 ^b	35.85 $\pm$ 492 ^b	48.78 $\pm$ 440 ^b	3.69 $\pm$ 0.29
CD	32.32 $\pm$ 496 ^a	6.52 $\pm$ 1.25	124.73 $\pm$ 13.05 ^a	24.59 $\pm$ 310 ^a	31.29 $\pm$ 506 ^a	4.07 $\pm$ 0.15
FD	27.42 $\pm$ 530 ^a	6.60 $\pm$ 0.87	110.36 $\pm$ 13.64 ^a	20.47 $\pm$ 391 ^a	27.23 $\pm$ 543 ^a	3.64 $\pm$ 0.34
$F_{3,39}$	3.106	0.786	3.076	3.662	4.172	0.352
P	0.037	0.509	0.039	0.020	0.012	0.788

CC: feeding on crickets with cricket-induced web vibratory stimuli; FF: feeding on flies with fly-induced vibratory stimuli; CD: feeding on crickets with fly-induced vibratory stimuli; FD: feeding on flies with cricket-induced vibratory stimuli; ($N = 11$ for each treatment). Values with different superscript letters are significantly different at 0.05 significance level; Fisher's least significant difference post hoc comparisons ($b > a$).

Table 2

Results of an ANCOVA test comparing stiffness of webs from four treatment groups with diameter and number of radii as covariates

Source	Type III sum of squares	df	Mean square	F	P
Intercept	1.286	1	1.286	8.132	0.007
Diameter of radii	0.013	1	0.013	0.081	0.777
No. of radii	0.095	1	0.095	0.603	0.442
Treatment	2.059	3	0.686	4.342	0.010
Error	6.007	38	0.158		

N = 11 for each treatment group.

that our assessment of cricket versus fly profitability is based on size and nutritional value and that the risks of foraging for few crickets compared to many flies also needs to be weighed up to assess the profitability of these prey comprehensively.

Coleopterans and hymenopterans dominate the diet of *N. pilipes* near our collection sites, orthopterans and dipterans being a relatively minor component (see Tso et al. 2005 for full details). Our dichotomous feeding regime therefore does not precisely reflect the prey experienced by these spiders in the wild. It does suggest, however, that *N. pilipes* builds webs aimed at capturing the largest and/or most profitable prey available in its immediate environment. Similar results have been obtained for an unrelated orb web spider, *Zygiella x-notata* (Venner & Casas 2005). It is thus conceivable that the strategy is widespread among orb web spiders. Furthermore, while prey nutrients and prey-induced web vibratory stimuli have separately been shown to influence orb web architecture (Landolfi & Barth 1996; Nakata 2007; Blamires et al. 2009; Mayntz et al. 2009), our study suggests that orb web spiders make decisions about altering their web architecture based on a combination of these cues.

Webs built by spiders fed live crickets had fewer radii and were considerably (approximately 1.6 times) stiffer than those of spiders fed live flies. The webs of spiders from the CC, FD and CD feeding regimes had fewer, shorter radii and greater mesh height, so were better at resisting the impacts of the higher kinetic energy prey, crickets. Greater spiral thread investment per capture area, as found for spiders from the FF treatment, are associated with webs aimed at capturing and retaining relatively small prey (Eberhard 1986; Sandoval 1994; Blackledge & Zevenberg 2006). Such webs use more silk and are more visible to predators and prey (Craig 1986; Venner et al. 2003); hence, they come at a cost.

As web vibrations assist in distinguishing prey, predators, mates or kleptoparasites (Barth 1985), the reduced signal clarity associated with webs of spiders in the FF treatment may render these spiders vulnerable to predators or kleptoparasites, or reduce the likelihood of detection of food or mates. Such sensory hindrance may be marked in *Nephila* because of their particularly small mesh height per capture area (Landolfi & Barth 1996; Tso et al. 2007). Vibration damping is thus an additional cost to building webs aimed at capturing flies compared to those aimed at capturing crickets. We accounted for mesh size in our procedures, so alterations in radial mechanics (e.g. stiffness, toughness) when feeding on flies (Tso et al. 2007) must explain the web-damping effect in the FF treatment. The profitability of a web-building strategy must none the less be considered in light of the behavioural and energetic circumstances faced by the spider. The relative ease of handling flies and the continuous intensity of fly vibrations, for example, may render the vibration damping ineffectual in the FF webs.

Spiral stickiness differed from the other web parameters we measured, as it was greatest in spiders that were fed dead crickets with fly vibratory stimuli (CD treatment group) than any other treatment group. The composition of the inorganic compounds in the aggregate (sticky) silks affects spiral stickiness in ecribellate orb web spiders and these may be altered when the spiders consume

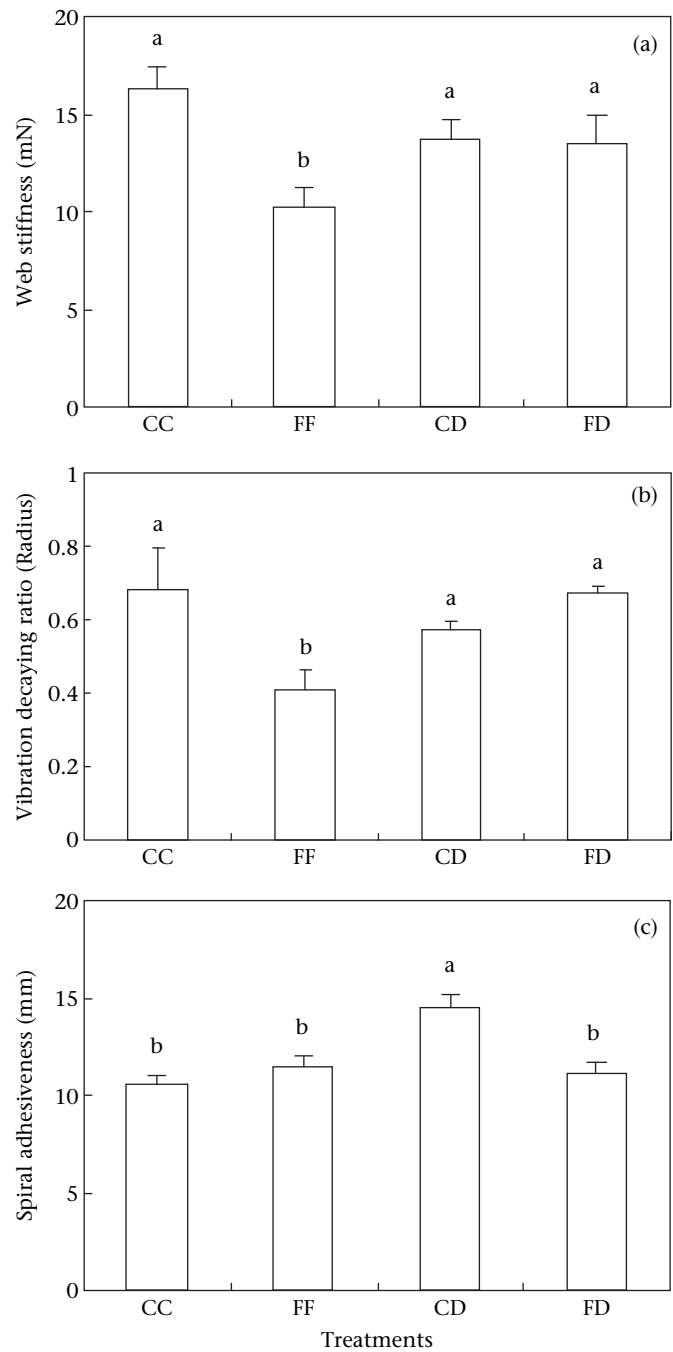


Figure 1. Mean + SE (a) stiffness, (b) vibration damping (%) and (c) spiral stickiness of webs built by *Nephila pilipes* in four treatment groups. CC: feeding on crickets with cricket-induced web vibratory stimuli; FF: feeding on flies with fly-induced vibratory stimuli; CD: feeding on crickets with fly-induced vibratory stimuli; FD: feeding on flies with cricket-induced vibratory stimuli. Different letters indicate significant differences between groups, a > b; least significant difference post hoc comparisons; N = 11 for each treatment in (a) and 5 for each treatment in (b) and (c).

Table 3

Results of an ANOVA test comparing vibration damping of webs from four treatment groups

Source	Sum of squares	df	Mean square	F	P
Treatment	0.139	3	0.046	3.849	0.03
Error	0.192	16	0.012		

N = 5 for each treatment.

Table 4

Results of an ANCOVA test comparing spiral silk stickiness of webs from four treatment groups with body length as the covariate

Source	Type III sum of squares	df	Mean square	F	P
Intercept	91.546	1	91.546	24.572	<0.001
Body length	1.223	1	1.223	0.328	0.570
Treatment	93.342	3	31.114	8.351	<0.001
Error	130.397	35	3.726		

N = 5 for each treatment group.

different prey types (Higgins et al. 2001; Townley et al. 2006). Nevertheless, nutrients cannot explain why cricket feeding with fly vibratory stimuli increased spiral stickiness in our experiment, as similar increases in spiral stickiness were not found in the webs of *N. pilipes* feeding on live and dead crickets. The stickiness of the spiral threads did not differ between spiders fed live crickets and live flies, so prey type does not seem to affect spiral stickiness. Receiving vibratory stimuli without reinforcement by feeding alters the stickiness of spiral threads of the orb web spider *Cyclosa octotuberculata* (Nakata 2007). Perhaps incongruence between the signal and the nutritional reinforcement elicits an anomalous behavioural or physiological response prior to the synthesis or deposition of aggregate silk. Further tests with cross manipulations of food and vibratory stimuli may ascertain when or how such a response occurs.

Prey nutritional and prey-induced web vibratory cues are not experienced by an orb web spider simultaneously with prey capture. The spider detects the web vibratory stimuli earlier than it does prey nutrients. Airborne vibratory stimuli may, additionally, be received by an orb web spider from the environment, which itself may be used to assess prey types (Sandoval 1994; Nakata 2007). The question remains therefore: why does *N. pilipes* rely on both web vibratory stimuli and nutrients as cues to assess prey in the environment? Recent studies have shown that prey nutrients influence the architecture and silk properties of spider orb webs because there is nutrient competition between silk synthesis, web building and somatic maintenance (Higgins & Rankin 1999; Mayntz et al. 2009; Blamires et al. 2009). It therefore appears that prey nutrients must be constantly assessed by spiders. Orb web architectural flexibility is thus a complex response involving consideration of more than the spider's foraging needs (Craig 2003). The precise influence of nutrients on web building in spiders, however, is relatively unexplored (but see Blamires et al. 2009; Mayntz et al. 2009) and more information is required to determine which nutrients act as cues, and how spiders partition nutrients between somatostasis and silk in order to understand how they mediate shifts in web architecture.

There is some evidence that prey removal or escape and/or web damage may influence the feeding behaviour or web architecture in orb web spiders (Venner et al. 2000; Nakata 2007). However, we did not consider it likely that the FD or CD treated *N. pilipes* responded to the removal and replacement of prey, or to vibrations generated in the course of these manipulations, rather than the treatments themselves since: (1) neither the CC nor the FF treatment group experienced any prey removal or damage, yet the FF group significantly shifted their web architecture; (2) we observed each spider feed and made no observations of any FD or CD spider altering its behaviour in response to the removal of initial prey; (3) the few tears made removing prey seemed too small for an alteration in web tension or vibratory propagation to be used as a cue to adjust web architecture; and (4) orb web spiders will continue to attack any object if stimulated appropriately by live prey. Replacing one cricket with five flies, and vice versa, was unlikely to induce marked changes in behaviour, as the flies were encountered simultaneously, in the same position in the web where the crickets

were encountered. It thus seems that our methods were successful at decoupling prey nutrients from prey-induced vibratory stimuli as effectively as possible and showed that *N. pilipes* uses nutritional and prey-induced vibratory cues in combination to assess its prey environment and to alter web architecture.

To summarize, our results are consistent with foraging models that suggest that predators target the most profitable prey in their habitat, switching strategies to target less profitable but more abundant prey only if the preferred prey becomes rare. We found that both prey-induced vibratory stimuli and prey nutrients are cues used by *N. pilipes* to assess the environment to make decisions about web architecture. We have expanded on work showing that *N. pilipes* alters its web architectural and silk properties according to its diet (Tso et al. 2005, 2007; Blamires et al. 2010). We found that when *N. pilipes* encounter less profitable prey, for example flies rather than crickets, over a period of time they build webs aimed at catching and retaining that prey. The fly-feeding webs may be more visible to predators and prey, so may be more costly. Future studies should aim to uncouple more cues, such as specific nutrients (e.g. protein versus lipids), allelochemicals, prey diversity and single versus multiple prey encounters.

Acknowledgments

We thank S. C. Wu, W. H. Lin, I. C. Chou, K. C. Chen, Y. H. Chang, J. C. Yang, H. Y. Lee and C. K. Yang for all sorts of assistance. This study was supported by grants from the National Science Council, Taiwan (NSC 97-2311-B-029-002-MY3, NSC 99-2621-B-029-002-MY3) and Council of Agriculture, Taiwan (94-9.1.7-e4(8)) to I.-M.T. and an NSC postdoctoral grant (NSC-98-2811-B-029-002) to S.J.B. We are grateful to M. Herberstein, T. Hesselberg and the anonymous referees for their constructive comments.

References

- Agarsson, I. & Blackledge, T. A. 2009. Can a spider web be too sticky? Tensile mechanics constrains the evolution of capture spiral stickiness in orb-weaving spiders. *Journal of Zoology*, **278**, 134–140.
- Askerland, D. R. 1994. *The Science and Engineering of Materials*. Boston: PWS Publishing.
- Barth, F. G. 1985. Neuroethology of the spider vibration sense. In: *Neurobiology of Arachnids* (Ed. by F. G. Barth), pp. 203–229. Berlin: Springer-Verlag.
- Bell, W. J. 1990. Searching behavior patterns in insects. *Annual Review of Entomology*, **35**, 447–467.
- Blackledge, T. A. & Zevenberg, J. M. 2006. Mesh width influences prey retention in spider orb webs. *Ethology*, **112**, 1194–1201.
- Blamires, S. J. 2010. Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology*, **213**, 3207–3212.
- Blamires, S. J., Hochuli, D. F. & Thompson, M. B. 2009. Prey protein influences growth and decoration building in the orb spider *Argiope keyserlingi*. *Ecological Entomology*, **34**, 545–550.
- Blamires, S. J., Chao, I. C. & Tso, I. M. 2010. Prey type, vibrations and handling interactively influence spider silk expression. *Journal of Experimental Biology*, **213**, 3906–3910.
- Blumstein, D. T. & Bouskila, A. 1996. Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos*, **77**, 569–576.
- Craig, C. L. 1986. Orb-web visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs within the Araneioidea. *Animal Behaviour*, **34**, 54–68.
- Craig, C. L. 2003. *Spiderwebs and Silks: Tracing Evolution from Molecules to Genes to Phenotypes*. Oxford: Oxford University Press.
- Eberhard, W. G. 1986. Effects of orb-web geometry on prey interception and retention. In: *Spiders: Webs, Behavior and Evolution* (Ed. by W. A. Shear), pp. 70–100. Stanford, California: Stanford University Press.
- Foelix, R. F. 1996. *Biology of Spiders*. 2nd edn. Oxford: Oxford University Press.
- Hansen, B. T., Holen, O. H. & Mappes, J. 2010. Predators use environmental cues to discriminate between prey. *Behavioral Ecology and Sociobiology*, **64**, 1991–1997.
- Heiling, A. & Herberstein, M. E. 2000. Interpretations of orb-web variability: a review of past and current ideas. *Ekologia*, **19**, 97–106.
- Herberstein, M. E. & Tso, I. M. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneioidea, Araneae). *Journal of Arachnology*, **28**, 180–184.

- Herberstein, M. E., Craig, C. L. & Elgar, M. E. 2000. Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evolutionary Ecology Research*, **2**, 69–80.
- Higgins, L. E. & Rankin, M. A. 1999. Nutritional requirements for web synthesis in the tetragnathid spider *Nephila clavipes*. *Physiological Entomology*, **24**, 263–270.
- Higgins, L. E., Townley, M. A., Tillinghast, E. K. & Rankin, M. A. 2001. Variation in the chemical composition of orb webs built by the spider *Nephila clavipes* (Araneae, Tetragnathidae). *Journal of Arachnology*, **28**, 82–94.
- Krebs, J. R. & Davies, N. B. 1987. *An Introduction to Behavioural Ecology*. 2nd edn. Oxford: Blackwell Scientific.
- Landolfi, M. A. & Barth, F. G. 1996. Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *Journal of Comparative Physiology A*, **179**, 493–508.
- Liao, C. P., Chi, K. J. & Tso, I. M. 2009. The effects of wind on trap structural and material properties of a sit-and-wait predator. *Behavioral Ecology*, **20**, 1194–1203.
- Masters, W. M., Markl, H. S. & Moffat, A. J. M. 1986. Transmission of vibration in a spider's web. In: *Spiders: Webs, Behavior and Evolution* (Ed. by W. A. Shear), pp. 49–69. Stanford, California: Stanford University Press.
- Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. & Simpson, S. J. 2005. Nutrient-specific foraging in invertebrate predators. *Science*, **307**, 111–113.
- Mayntz, D., Toft, S. & Vollrath, F. 2009. Nutrient balance affects foraging behaviour of a trap-building predator. *Biology Letters*, **5**, 735–738.
- Nakata, K. 2007. Prey detection without successful capture affects spider's orb-web building behaviour. *Naturwissenschaften*, **94**, 853–857.
- Nakata, K. 2008. Spiders use airborne cues to respond to flying insect predators by building orb-web with fewer silk thread and larger silk decorations. *Ethology*, **114**, 686–692.
- Nakata, K. 2010. Attention focusing in a sit-and-wait forager: a spider controls its prey detection ability in different web sectors by adjusting thread tension. *Proceedings of the Royal Society B*, **277**, 29–33.
- Opell, B. D., Lipkey, G. K., Hendricks, M. L. & Vito, S. T. 2009. Daily and seasonal changes in the stickiness of viscous capture threads in *Argiope aurantia* and *Argiope trifasciata* orb webs. *Journal of Experimental Zoology*, **311A**, 217–225.
- Page, R. A. & Ryan, M. J. 2005. Flexibility in assessment of prey cues: frog-eating bats and frog calls. *Proceedings of the Royal Society B*, **272**, 841–847.
- Parry, D. A. 1965. The signal generated by an insect in a spider's web. *Journal of Experimental Biology*, **43**, 185–192.
- Sandoval, C. P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*, **8**, 701–707.
- Sherman, P. M. 1994. The orb web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*, **48**, 19–34.
- Toft, S. & Wise, D. H. 1999. Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. *Oecologia*, **119**, 198–207.
- Townley, M. A., Tillinghast, E. K. & Neefus, C. D. 2006. Changes in composition of spider orb web sticky droplets with starvation and web removal and synthesis of sticky droplet compounds. *Journal of Experimental Biology*, **209**, 1463–1486.
- Tso, I. M. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. *American Midland Naturalist*, **141**, 238–246.
- Tso, I. M., Wu, H. C. & Hwang, I. R. 2005. Giant wood spider *Nephila pilipes* alters silk protein in response to prey variation. *Journal of Experimental Biology*, **208**, 1053–1061.
- Tso, I. M., Chiang, S. Y. & Blackledge, T. A. 2007. Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? *Ethology*, **113**, 324–333.
- Venner, S. & Casas, J. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society B*, **272**, 1587–1592.
- Venner, S., Pasquet, A. & Leborgne, R. 2000. Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Animal Behaviour*, **59**, 603–611.
- Venner, S., Bel-Venner, M. C., Pasquet, A. & Leborgne, R. 2003. Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften*, **90**, 269–272.
- Zschokke, S. 1999. Nomenclature of the orb-web. *Journal of Arachnology*, **27**, 542–546.