



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

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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 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.

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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

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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

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