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Signals and Signal Choices made by the Araneophagic Jumping Spider *Portia fimbriata* while Hunting the Orb-Weaving Web spiders *Zygiella x-notata* and *Zosis geniculatus*

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Abstract

Portia fimbriata is a web-invading araneophagic jumping spider (Salticidae). The use of signal-generating behaviours is characteristic of how *P. fimbriata* captures its prey, with three basic categories of signal-generating behaviours being prevalent when the prey spider is in an orb web. The predatory behaviour of *P. fimbriata* has been referred to as aggressive mimicry, but no previous studies have provided details concerning the characteristics of *P. fimbriata*'s signals. We attempt to determine the model signals for *P. fimbriata*'s 'aggressive mimicry' signals. Using laser Doppler vibrometer and the orb webs of *Zygiella x-notata* and *Zosis geniculatus*, *P. fimbriata*'s signals are compared with signals from other sources. Each of *P. fimbriata*'s three categories of behaviour makes a signal that resembles one of three signals from other sources: prey of the web spider (insects) ensnared in the capture zone of the web, prey making faint contact with the periphery of the web and large-scale disturbance of the web (jarring the spider's cage). Experimental evidence from testing *P. fimbriata* with two sizes of lure made from *Zosis* (dead, mounted in a lifelike posture in standard-size orb web) clarifies *P. fimbriata*'s signal-use strategy: (1) when the resident spider is small, begin by simulating signals from an insect ensnared in the capture zone (attempt to lure in the resident spider); (2) when the resident spider is large, start by simulating signals from an insect brushing against the periphery of the web (keep the resident spider out in the web, but avoid provoking from it a full-scale predatory attack); (3) when walking in the resident spider's web, regardless of the resident spider's size, step toward the spider while making a signal that simulates a large-scale disturbance of the web (mask footsteps with a self-made vibratory smokescreen).

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Introduction

Although mimicry has long been a major topic in biology, aggressive mimicry, where the predator deceives its prey, has received less attention than Batesian mimicry, where the prey deceives the predator (Wickler 1968). The classic example of aggressive mimicry may be the angler fish which attracts its prey, a smaller fish, into striking distance with a protuberance on its head that resembles the prey of the angler fish's own prey (Gudger 1946). In this example, the cues to which the tricked prey responds are presumably optical. Araneophagic spiders are of interest because they appear to provide examples of aggressive mimicry based on a different sensory modality, web signals. Also, araneophagic spiders, especially araneophagic jumping spiders (Salticidae), appear to practise a more flexible style of aggressive mimicry than that found in the angler fish.

Salticids are exceptional spiders because they have acute eyesight (Land 1985; Jackson & Blest 1982b). Most salticids prey primarily on insects and do not build webs (Jackson & Pollard 1996). Some salticids opportunistically practise araneophagy by walking or, more often, leaping into the webs of other spiders (Jackson 1986). More specialized araneophagy is practised by a smaller group of salticids. After entering another spider's web, these salticids do not merely stalk the resident. Instead, they vibrate the web with their legs and palps in a way that makes web vibratory signals that apparently manipulate the behaviour of the resident spider, sometimes drawing it close enough to be attacked (Wilcox & Jackson 1998). Therefore, it has been suggested that this tactic of capturing web spiders is a form of aggressive mimicry. Only four salticid genera (*Brettus*, *Cyrrba*, *Gelotia* and *Portia*), all of which are in the subfamily Spartaeinae, are known to practise this predatory tactic (Jackson & Pollard 1996). *P. fimbriata* has been the most extensively studied species from the four genera, with Queensland *P. fimbriata* being the population about which we have the most information (Jackson & Pollard 1996).

The web spiders on which *P. fimbriata* preys, having poor eyesight, perceive the world around them primarily by interpreting vibratory web signals (Homann 1928; Barth 1982, 1985, 1986; Foelix 1982). It has been argued that *P. fimbriata*'s success at araneophagy depends largely on being able to orchestrate the pattern of web signals received by the resident spider (Jackson & Wilcox 1998). With eight legs and two palps, all of which can move independently of each other at different and variable amplitudes and velocities, details of *P. fimbriata*'s signal-generating behaviours when on other spiders' webs tend to be complex (Jackson & Blest 1982a; Jackson & Wilcox 1994). However, it is not straightforward to conclude from this that the actual web signal transmitted to the resident spider also varies.

P. fimbriata's signal-generating behaviours can be categorized into three basic modes, based upon how *P. fimbriata* manipulates the silk (Jackson & Pollard 1996):

(1) steady, strong silk manipulation, where *P. fimbriata* makes sustained (1 s or longer) up-and-down movements of its palp legs or both of its palps and its legs (generally $2\text{--}4\text{ s}^{-1}$; amplitude typically 1–2 mm); (2) faint silk manipulation, where *P. fimbriata* intermittently moves one or more of its appendages (legs, palps or both legs and palps) briefly (for less than 1 s) and slowly ($1\text{--}2\text{ s}^{-1}$) up and down (typically at an amplitude of less than 1 mm); (3) brief, strong rocking of the web, where *P. fimbriata* suddenly and rapidly flexes most or all of its legs at high amplitude, making its body rock violently up and down on the web for about 1 s. This body rocking is often accompanied by *P. fimbriata* making an initial lunge forward, and *P. fimbriata* is always completely in the web when this behaviour mode is used.

It has been suggested *P. fimbriata*'s strategy is based on a combination of ploys. Signals that simulate a small insect ensnared in the resident spider's web may be used when the resident spider is relatively harmless (e.g. small) (Jackson & Blest 1982a; Jackson & Hallas 1986a). However, when faced with a more dangerous (e.g. larger) quarry, *P. fimbriata* may send signals that are ambiguous, thereby keeping the resident spider out in the web where it can be stalked, but not provoking a potentially lethal full-scale predatory attack (Wilcox & Jackson 1998). When close, *P. fimbriata* may mask its footsteps under a self-made vibratory smokescreen by making large-scale signals that simulate extraneous 'noise' in the web such as wind or vegetation falling on the web (Wilcox & Jackson 1998). However, there have been no previous investigations of these hypotheses.

An understanding of the physical characteristics of the web signals made by *P. fimbriata*, and a comparison of these signal with other web signals normally encountered by the resident spider, is essential. The situation of aggressive mimicry by *P. fimbriata*, in the medium of web-signal cues, is different from the situation with the angler fish, where aggressive mimicry is in the medium of optical cues. Although optical cues tend to be evident to us, animal eyes differ considerably (e.g. have sensitivity to different wavelengths of light; Land 1985), and so it is not even safe to assume that what we see is what the angler fish's prey sees. The physics of vibratory-signal transmission in webs being complex and not well understood (Landolfi & Barth 1996; Barth, pers.comm.), the problem is here even more complex: we cannot simply look at an interaction between *P. fimbriata* and its prey and see what cues are relevant to the prey spider.

The expression 'aggressive mimicry' would seem to imply that *P. fimbriata*'s signals are deceptive, resembling other naturally occurring web signals (the models in this mimicry system), but there have been no previous publications that compare *P. fimbriata*'s signals with potential model signals. In this, the first study to make such comparisons, we use orb webs as a case study to address the question of match-ups between *P. fimbriata* and model signals. Using laser Doppler vibrometry (LDV), we determine the signal characteristics in a web-based aggressive system for the first time, and we also investigate experimentally previously proposed, but not tested, hypotheses concerning the situations in which *P. fimbriata* uses its different types of signalling.

More specifically, in our investigation of signal characteristics, we consider

two questions. (1) When *P. fimbriata* performs its three different modes of signal-generating behaviour, are three corresponding different types of signal transmitted through the web? This should not be simply assumed. First we need to rule out an alternative hypothesis, that no matter which mode of signal-generating behaviour *P. fimbriata* uses, the signals generated are essentially the same. (2) Can we identify specific model signals that justify calling *P. fimbriata*'s signalling 'aggressive mimicry'? Our hypothesis is that, when adopting a particular one of the three modes of signal-generating behaviour, *P. fimbriata* simulates a particular one of the following: (a) the strong signals made by a prey ensnared and struggling in a web ('prey simulation signals'); (b) the faint, uncertain signals made by a prey contacting the periphery of the web ('ambiguous signals'); (c) large-scale disturbances made when the web is shaken by the wind or hit by a large object ('self-generated smokescreen signals').

The prey-simulation hypothesis was emphasized in early studies (Jackson & Blest 1982a; Jackson & Hallas 1986a), and was suggested by the way in which the resident spider often reacts when *P. fimbriata* uses its appendages to make large displacements of web silk: the resident spider may rush toward the signalling *P. fimbriata* in more or less the same manner as when attacking an ensnared insect. However, prey simulation is a risky tactic, and it has been hypothesized, based on behavioural observations, that *P. fimbriata* often may make only faint, ambiguous signals, which provoke no more than investigative behaviour from the resident spider, instead of a full-scale attack (Jackson 1995; Jackson & Pollard 1996; Jackson & Wilcox 1998).

The manner in which orb-weaving spiders react to ambiguous information is particularly well known. For example, orb weavers often 'probe' (using legs to tighten the tension of web lines) and 'pluck' (using legs to make sudden jerks on web lines). It has been hypothesized that probing enhances the web's signal-transmission properties, and plucking the web may facilitate prey location by providing the resident spider with a vibratory echo (Klärner & Barth 1982; Landolfi & Barth 1996). Another common response of orb-weaving spiders is to pull on web silk while orienting and moving a few steps toward the source of the ambiguous signal (Liesenfeld 1956; Lubin 1986). Since these investigative behaviours are similar to how spiders sometimes react to *P. fimbriata*'s signals, it has been suggested (as already mentioned) that *P. fimbriata* sometimes generates ambiguous signals in order to draw a prey spider slowly closer.

The self-generated smokescreen hypothesis is derived again from behavioural observations of *P. fimbriata* attempting to walk through a web in order to get within striking distance of the web spider. When doing so, *P. fimbriata* has a bias to step across the web toward the resident spider, especially when an outside disturbance, such as a passing breeze, causes large-scale disturbance of the web silk (Wilcox & Jackson 1996). Large-scale disturbances caused by, for example, the wind, stray objects hitting the web, or an animal bumping into or brushing up against the vegetation to which the web is anchored, tend to be ignored by the resident spider (Liesenfeld 1956; Hoffmaster 1982; Masters 1984a). Evidently, these disturbance signals also mask the faint signals made by *P. fimbriata*'s stepping.

Therefore, this tactic has been called an 'opportunistic smokescreen tactic'. However, it has been hypothesized that *P. fimbriata* also generates 'self-made smokescreens', whereby *P. fimbriata*, when walking across a web, cloaks its own footsteps by making large-amplitude masking signals which resemble the naturally occurring signals routinely ignored by the resident spider (Wilcox & Jackson 1996, 1998).

To investigate these three hypotheses, we compared the signals made by *P. fimbriata* with the stated model signals: struggles made by small insects ensnared in the catching zone of the spider's web (ensnared-prey signals), small insects making light contact with the peripheral regions of the web (peripheral-contact signals), and large-scale disturbances of the whole web (smokescreen). For smoke-screen signals, we aimed to obtain disturbances that imparted energy to the web sufficient to make the web vibrate at its resonating frequency.

Spiders are known to rely especially on frequency components of signals (Hergenröder & Barth 1983; Master 1984b). Our goal was to determine the frequency spectra of each of these model signals and to compare them to the spectra of *P. fimbriata*'s putative aggressive mimicry signals. The rationale was that, if *P. fimbriata*'s tactic is, as hypothesized, to imitate a particular category of signal, then the spectra should match.

The types of web built by spiders are highly diverse, ranging from sparsely woven three-dimensional space webs, through highly organized two-dimensional orb webs, to densely woven sheet webs (Shear 1994; Foelix 1982). For this initial study, we chose the orb-weaving spiders *Zygiella x-notata* and *Zosis geniculatus* as prey. The highly ordered design of an orb web (and the fact that all LDV studies on web vibrations have been performed on orb webs) makes this the most convenient and tractable type of web for recording signals with a LDV. Orb webs are essentially two-dimensional sheets of silk strung under high tension. An orb web consists of four different components: the frame, radius, hub and sticky spiral, arranged in a pattern that, in some ways, resembles that of a bicycle wheel (Fig. 1). The radials radiate outward from a central position (the hub) and are anchored to the frame, which is itself in turn anchored to the surrounding vegetation by means of anchor strands that support the entire structure. The sticky spiral winds out across the radii from the hub to the frame. The sticky spiral is the principle structure for capturing prey, and gets its name from the fact that the silk of the spiral is adhesive, sticking to anything that touches it. The region of the web covered by the sticky spiral is often called the 'catching zone'.

Additionally, some species build a stabilimentum of thick silk at or around the hub of the web. The shape of the stabilimentum varies from species to species; sometimes it is shaped as a cross, sometimes as a ring around the hub. What function stabilimenta perform is not clear.

Although *Zygiella*'s and *Zosis*' webs, being orb webs, are similar in design, there are some major structural differences between the two. *Zygiella* spins an ecribellate sticky orb, whereas *Zosis* spins a cribellate orb. For cribellate orb-weaving spiders, the sticky spiral consists of a line of silk wrapped in a very fine wool of threads spun from a structure located near the spinnerets called a cribellum.

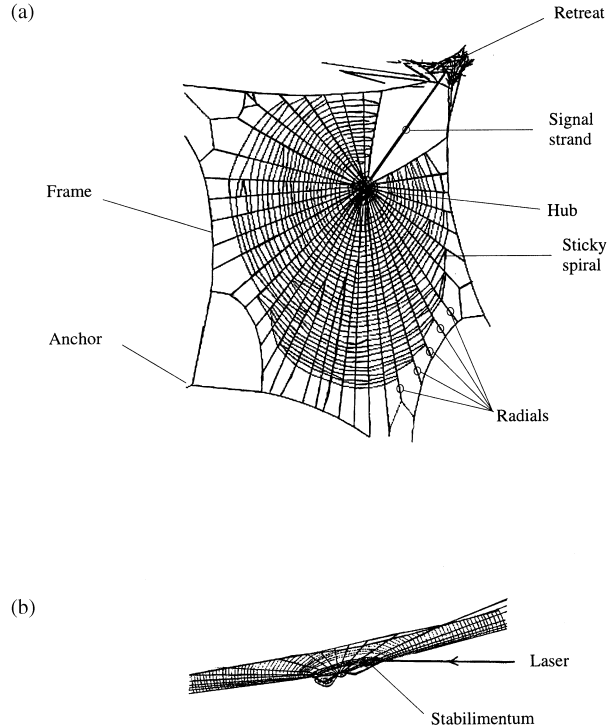


Fig. 1: (a) *Zygellia*'s web. *Zygellia* spends most of the day in its retreat off the web, while monitoring vibrations in the web through the signal strand that runs from its retreat to its nest (the figure is a modified version of that in Foelix 1982). (b) *Zosis* and its web. *Zosis* builds a horizontally or diagonally oriented cribellate orb web, and sits in the middle of the web, elongated so that its first pair of legs is stretched out in front of it to rest on the outermost part of the web's stabilimentum. The figure shows how laser light was focused on the point where *Zosis*' first pair of legs contact the stabilimentum

Why cribellate silk is sticky is not clear. Ecribellate orb-weaving spiders, however, string droplets of fluid glue along the silk of the sticky spiral at regular intervals.

Another major structural difference between the two webs is that *Zygiella*'s orb is usually oriented nearly vertically, whereas *Zosis*' web is usually oriented more or less horizontally (Fig. 1). Yet another difference is that *Zosis* builds a stabilimentum of thick silk surrounding the hub whereas *Zygiella* does not.

Still another difference between the two species is the spider's location in the web. *Zosis*, like most orb weavers, rests at the hub; it hangs upside down in the middle of the stabilimentum, its two front legs together resting on the junction between the stabilimentum and one of the radial lines (Fig. 1). *Zygiella*, however, stays in a nest off the web. In order to monitor what occurs in the web, it attaches a signal line between its nest and the hub of the web, running the signal line through a sector of the orb free of silk (Fig. 1).

Living off the web makes *Zygiella*'s attack behaviour distinctive. When prey

on the spiral is detected, *Zygiella* rushes down the signal thread to the hub and then to the prey. Its probing behaviour consists of the spider extending one leg of its front pair to grab and pull on the signal strand (Liesenfeld 1956; Klärner & Barth 1982) while also usually coming out of its nest a short distance along its signal strand. The attack behaviour of *Zosis* is also distinctive. When an insect is detained by the silk of the spiral, *Zosis* rushes to it and begins aggressively wrapping the prey. While hanging underneath the web by its third pair of legs, *Zosis* rapidly rotates the prey while holding it close to its spinnerets. In a short time, the large amounts of silk wrapped around the prey immobilize it completely.

Zosis' probing is also distinctive. *Zosis*' web normally sags, apparently as a consequence of the spider hanging from the web underneath it. When *Zosis* detects something in its web, it probes by pulling on the web with its front pair of legs, thereby taking the slack out of the sticky spiral and presumably improving its signal transmission properties. When *Zosis* pulls, the spiral (and the spider) is lifted upward. When the spider releases its pulled-on silk, the spiral sags again. *Zosis* can cause the spiral to bounce up to 10 times per second. This behaviour is called 'web tensioning' or 'web pulling' (Lubin 1986), depending on the rapidity with which the spider bounces in its web.

Another reason for choosing *Zygiella* and *Zosis* as prey items with which to test *P. fimbriata* was to maximize the chance of getting *P. fimbriata* to vary its signalling behaviour during recording sessions. Although *P. fimbriata* appears to be biased toward using, at least initially, different particular signalling behaviour on different types of commonly encountered web (Jackson & Pollard 1996), we minimized the likelihood of this by choosing *Zygiella x-notata* and *Zosis geniculatus*. *Zygiella* is not sympatric with *P. fimbriata*. *Zosis geniculatus* is, but it appears to be a rare prey for *P. fimbriata*. By using these two species of orb weaver, we aimed to obtain a measure of the behaviour of *P. fimbriata* in encounters with orb-weaving spiders, rather than its behaviour with any particular species of prey.

Materials and Methods

Vibration Tests

Standard housing and maintenance procedures for *P. fimbriata* were used (Jackson & Hallas 1986a), in a controlled-environment laboratory (light/dark cycle: 12/12 h). Lights came on in the laboratory at 08:00 h.

Except where it would cause confusion, each species tested is referred to by its genus. We housed each web spider in a different cage, with dimensions of either 300 × 300 × 300 mm or 100 × 100 × 100 mm, depending on the size of the web spider. These cages were made of wood, with a removable perspex front and back. For the large cages, six 1-cm-diameter holes were drilled, two each, through the middle of the two opposite sides and the ceiling of each cage. For the small cages, two holes, each 3 mm in diameter, were drilled through the ceiling. These holes were used to drop prey in to feed the spider. When the spiders were not being fed, these holes were plugged.

We used a laser Doppler vibrometer (LDV) to measure web vibrations. An LDV uses the Doppler shifts of light reflected off an object to measure the velocity of the moving object (for details, see Buchhave 1975), and has been used before to measure web vibrations (Masters & Markl 1981; Masters et al. 1982; Masters 1984a, b; Landolfi & Barth 1996). Because the LDV measures the velocity of an object, not its displacement, the amplitudes in our results are presented as m s^{-1} (peak to peak).

The cage containing the spider to be tested was placed on a standard vibration-proof table designed to reduce stray ground-transmitted vibrations. Furthermore, in order to limit the effect of stray draughts on the web, we positioned the cage in the middle of a $50 \times 50 \times 50$ cm wooden box with an open front. We video-taped the spiders' behaviours. The vibrations measured by the laser were recorded simultaneously on DAT and on the soundtrack of the video-tape. The DAT record was used for signal analysis, while the video-tape soundtrack was used for the synchronization of the DAT with the video. In this way, we were able to correlate the behaviour *P. fimbriata* used to make a signal with the signal the behaviour made. A Cambridge Electronic Design (CED; Cambridge, UK) A/D converter was used to translate the signal to a 586 computer, where it was sampled at 4000 Hz and analysed using an FFT algorithm from a program provided by CED.

No matter how stringent the recording conditions, one cannot completely eliminate the effect of stray ground and wind-borne vibrations, especially in an ultra-lightweight structure such as a web. Therefore, to obtain the true signal produced by an object, we measured the 'background' vibrations of the web before each test, and subtracted the spectra produced by these vibrations from the spectra of the signals produced by an object (e.g. a fly or *P. fimbriata*). (This technique is analogous to recording the 'background radiation' before determining whether a nuclear power plant is spewing radioactivity.)

During the course of the study we found that, even within the course of a single recording session (e.g. recording a single *Drosophila* in a web), there was a degree of variation in both the frequency and the amplitude of the signals produced. Therefore, we computed an 'average spectrum' for each experiment that we ran. To do this, we first found the spectrum for every signal recorded during an experiment. We then subtracted the 'background spectrum' we recorded at the start of the test (see above) from each of these signal spectra. From these 'calibrated' spectra, we then found the average amplitude of the signal at each frequency. From these average amplitudes, we constructed the average spectrum for the signals recorded during the experiment. Each spectrum presented in the results is an average spectrum, and the number of signals (n) that went into each calculation is given alongside it.

Three basic types of web vibration are discernible in webs (Masters 1984a): translational, or those which move perpendicular to the long axis of the silk but within the plane of the web; lateral, or those that move perpendicular to the long axis of the silk and to the plane of the web, and longitudinal, or the compression waves that move along the long axis of the silk. [Rotational vibrations (where silk rotates along its long axis) probably also exist, but no technique has yet been

worked out for quantitatively measuring these vibrations.] Longitudinal vibrations seem to be the most important type of vibration for the web spider: they are transmitted better than the others through the web and the amplitude of the vibrations needed for unleashing a spider's predatory attack is lower for longitudinal vibrations than for any other (Klärner & Barth 1982; Masters 1984a,b). We therefore concentrated our study on these types of vibration.

When testing *Zygiella*, we measured the longitudinal vibrations at the hub of the web along a vector that was as near as parallel to the long axis of the signal strand as we could get it. To do this, we used a mirror positioned to reflect the light of the laser up along the axis of the signal strand (Fig. 2). When testing *Zosis*, the laser was focused on the stabilimentum where the front pair of legs contact the radius. This enabled us to measure the back-and-forth movements of the junction of the radius with the stabilimentum (Fig. 2). In this study, we provide for the first time recordings of prey vibrations in *Zygiella* webs using an LDV. Also, our recordings from *Zosis*' web are the first, using any method, for a cribellate orb web.

Recording Potential Model Signals for *P. fimbriata*'s Putative Aggressive Mimicry Signals

Three basic types of signal were recorded. For the potential model of *P. fimbriata*'s smokescreen signal, we made large-scale energy inputs into the webs of *Zygiella* and *Zosis* by dropping a 50-g weight on the centre of the top of the cage with a force equal to 1.5×10^{-4} N. After experimenting with various other methods (e.g. throwing balls of paper into the web or generating artificial wind gusts), this technique was determined to be the most effective for setting off whole-web vibration at the resonating frequency. It provided a repeatable, precise force that would rock the entire web. Although it may at first seem as if we would be measuring the resonance frequencies of the box with such a technique, the truth is that, although the force of the impact would be transferred to the wooden box and then to the web, the much greater stiffness of the wooden box in comparison to

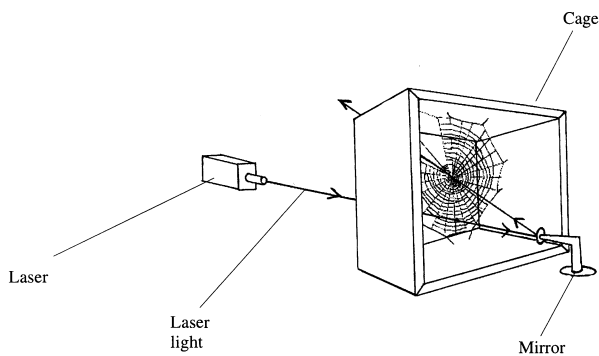


Fig. 2: How a mirror was used to orient the laser so that longitudinal vibrations of the hub along the parallel near to axis of the signal strand could be measured

the elastic web would ensure that the vibrations of the box caused by knocking on it would come to rest much sooner than those of the web. Therefore, the energy caused by banging on the box will be transferred to the web, but the web will vibrate freely at its own resonance frequency, and not at those of the box. An analogous situation is what would happen if you were to drop a Steinway piano; the box and frame to which the strings are attached would make a short, dull 'thump', whereas the strings themselves would vibrate at their own resonance frequencies for a much longer period of time.

To record the signals made by prey caught in the sticky spiral of the web, we knocked out the fly with CO₂ and used forceps to place it in the web on a sticky strand near a radial, being careful not to damage the web in the process. Damaged webs were not tested. We began recording when the fly came around and began struggling. 'Peripheral' prey vibrations were recorded by placing either a vestigial-winged *Drosophila* (*Zygiella*) or *Musca* (*Zosis*) on the floor of the cage and having them simply walk about. Eventually, the fly would come into contact with an anchor strand and produce a signal.

Recording Signals Made by *P. fimbriata*

When tested with spiders in the large cage, *P. fimbriata* was introduced through one of the holes in the bottom of the cage. When tested with spiders in the small cage, *P. fimbriata* was introduced into the cage through the front. Regardless, *P. fimbriata* was allowed to walk freely into the cage. Recording of the tests began as soon as *P. fimbriata* entered the cage. Tests ended when either *P. fimbriata* caught the prey, *P. fimbriata* left the cage, or the prey spider fled from *P. fimbriata* and did not return to its web or nest.

We categorized each signal according to the mode of signal-generating behaviour *P. fimbriata* used to generate the signal, and found the average spectrum for each mode.

Behavioural Tests with Dead *Zosis*

In our second set of experiments, we wanted to see whether *P. fimbriata* uses different types of signal under different predatory conditions. For these experiments, we examined which signals *P. fimbriata* would use while attacking differently sized lures made from dead *Zosis*. Because we used dead *Zosis*, it was impossible for *P. fimbriata*, from a position at the edge of the web, to lure the animal closer to itself by triggering either a predatory attack or a slow approach. When *P. fimbriata* fails to draw a web spider closer, it tends to enter the web and walk toward the spider. In this way, we were able to lure *P. fimbriata* out onto the web and thus see if it would use a different set of vibrations when in the web approaching the lure than when at the edge of the web.

These tests were conducted in cages made from cubicle wood frames with four sliding glass (transparent) sides (internal dimensions of chamber: 95 mm on each side). There was a hole (the introduction site) centred on the wooden bottom of the cage. This hole was used for introducing *P. fimbriata* at the start of a test.

The test chamber was set on top of a 95-mm² base open underneath so that the introduction site could be easily reached.

Lures were made from dead *Zosis* mounted in a lifelike posture and placed at the hub of the web. Two sizes of lure were used, small (≈ 3 mm in body length), and large (≈ 7 mm in body length). Placing a dead *Zosis* directly in the web proved very difficult: the legs of the spider tended to get snagged in the web, and become distorted out of position; furthermore, the dead spider often fell out of the web. Therefore, we mounted each dead spider on the centre of one side of a disk-shaped piece of cork (diameter ≈ 0.5 times the body width of the *Zosis*). Cork was used because the surface of the cork adhered readily to the sticky (cribellate) silk in *Zosis*' web. Lures were made by killing the *Zosis* by asphyxiation with carbon dioxide, then placing it in alcohol for 60 min. Afterwards the lure was mounted by its sternum (underside of the cephalothorax) onto the cork and its legs placed in a lifelike posture. The cork and spider were then sprayed with an aerosol plastic adhesive for preservation and elimination of potential olfactory cues from the dead spider.

The lure was placed in the centre of a web obtained by putting an adult female *Zosis* into the cage 4 d before the experiment. During this 4-d web-building period, no prey were provided to the *Zosis*. On the day of the experiment, one or more of the sides were removed from the cage and the living *Zosis* gently prodded out of its web and removed from the cage. If the web was noticeably damaged during this process, it was not used. Instead, the cage was cleaned and a new *Zosis* was put inside for another 4 d. The lure was then placed carefully on the hub of the web. Sometimes, the legs of the lure got caught on the silk and were pulled into a non-lifelike position. When this happen, the lure was not used. The cage, web and lure were used only if we were successful in putting the lure into the web in a lifelike posture without visibly damaging the web in the process.

We tested *P. fimbriata* juveniles which were ≈ 7 mm in body length. Each *P. fimbriata* was tested only once. The size of the lure with which a *P. fimbriata* was tested was decided at random.

Tests always started at *c.* 10:00 h and began with the *P. fimbriata* to be tested being placed in a transparent plastic tube with a diameter of 10 mm. About 5 min later, one end of the tube was connected to a hole in the bottom of the cage and the other end was plugged with a cork. The *P. fimbriata* could thus enter the cage by walking up out of the tube. Once the *P. fimbriata* entered the cage (usually within 10 min of the tube being connected to the hole in the bottom of the cage), the tube was removed and the hole in the cage was plugged with a cork.

Tests had a maximum duration of 4 h. If, after 4 h, the *P. fimbriata* made no contact with the web, the test was aborted. The only way we allowed *P. fimbriata* to contact the web was by stepping onto it. Therefore, tests were also aborted if *P. fimbriata* leapt into the web instead of stepping onto it, or if *P. fimbriata* dropped on a dragline toward the web from above. If a test was aborted, the individual *P. fimbriata* was tested again on successive days (for a maximum of 4 d) until a successful test was achieved. In the tests of *P. fimbriata* with large *Zosis*, the test was aborted once for four *P. fimbriata*, aborted twice for two *P. fimbriata* and

aborted four times for one *P. fimbriata*. In the tests of *P. fimbriata* with small *Zosis*, the test was aborted once for six *P. fimbriata*, aborted twice for one *P. fimbriata* and aborted three times for one *P. fimbriata*.

Once *P. fimbriata* contacted the web, the first behaviour it used to make a vibratory signal was recorded (i.e. the manner in which *P. fimbriata* moved its appendages was written down). If *P. fimbriata* left the web without signalling, observation was continued for the full 4 h. If *P. fimbriata* returned to the web during this period and started signal-making behaviours, these signals were recorded as *P. fimbriata*'s first signals.

After entering the web, many *P. fimbriata* approached the lure. However, tests ended when *P. fimbriata* came within 20 mm of the lure or when the 4-h test period was over; no *P. fimbriata* was allowed to contact the lure. If *P. fimbriata* approached the lure, the near-lure signalling behaviour was recorded. The near-lure signalling behaviour was defined as either the behaviour *P. fimbriata* used after closing to within 20 mm of the lure, or the last behaviour *P. fimbriata* used during the 4-h testing period provided that *P. fimbriata* had closed to within 50 mm of the lure. If *P. fimbriata* did not signal when within this 20–50 mm window, then the result was recorded as 'no signal when near lure'.

Results

Signals in *Zygiella*'s Web

In *Zygiella* webs, large-scale disturbances produced signals with a simple waveform whose frequency spectra showed a single amplitude peak at frequencies between 10 and 20 Hz (Fig. 3a). *Drosophila* entrapped in the sticky spiral produced signals with a more complicated waveform whose spectra showed two amplitude peaks, one between 10 and 20 Hz (the same frequency range seen for large-scale disturbances) and one between 35 and 100 Hz (Fig. 3b). The peak amplitudes of the frequencies between 10 and 20 Hz and between 35 and 100 Hz were approximately equal. *Musca* caught in the sticky spiral produced signals with frequencies whose amplitudes peaked at almost identical frequencies to those of the signals produced by *Drosophila*: one peak amplitude between 10 and 20 Hz and another between 45 and 75 Hz (Fig. 3c). In fact, when tested within the same web, the average spectra from *Musca* and *Drosophila* had almost identical shapes except that, in *Musca*, the peak amplitude between 10 and 20 Hz was greater than the peak amplitude between 45 and 75 Hz.

Drosophila brushing up against an anchor thread produced a very faint 'clicking' noise (Fig. 3d) of an instantaneous duration. These signals occurred very irregularly, sometimes individually and sometimes in groups, and produced spectra showing amplitudes which peaked at 300, 500 and 800 Hz.

Signals in *Zosis* Webs

Large-scale disturbances in *Zosis* webs produced signals similar to those produced by large-scale disturbances in *Zygiella* webs, their frequency spectra showing a single, large amplitude peak below 30 Hz (Fig. 4a).

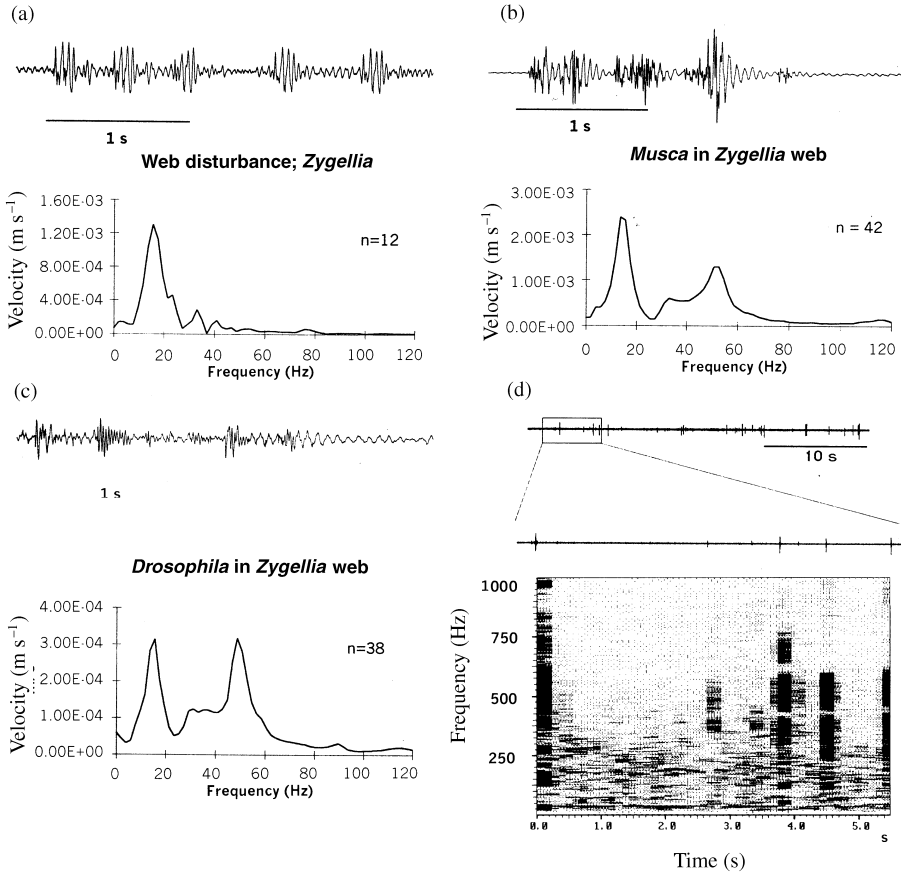


Fig. 3: Results for *Zygellia*. (a) Top: signals created by 'whole-web' disturbances (i.e. knocking on the outside of the cage by dropping a 50-g weight on top of the cage); bottom: average spectrum of these signals. (b) Top: signals made by *Musca* caught in the web's sticky spiral; bottom: average spectrum. (c) Top: signals made by *Drosophila* caught in the web's sticky spiral; bottom: average spectrum. (d) Top: signals made by *Drosophila* brushing up against the web's anchor strands; bottom: sonagram of the signal

The signals made by *Musca* in *Zosis*' sticky spiral were impossible to record because the fly created sustained vibrations that caused the entire web to shake at amplitudes even greater than those cause by knocking on the web. These oscillations made it impossible to keep the laser focused on the web. *Zosis* reacted to these signals by either ignored the fly or fleeing from its web.

We also had problems recording the signal made by *Drosophila* caught in *Zosis*' sticky spiral. When tested with *Drosophila* in the spiral, *Zosis* reacted immediately with web-tensioning and web-pulling, followed soon after with an attack. Because web-tensioning and web-pulling repeatedly caused the sticky spiral of the web to change position (see above), there was again no way to keep the laser

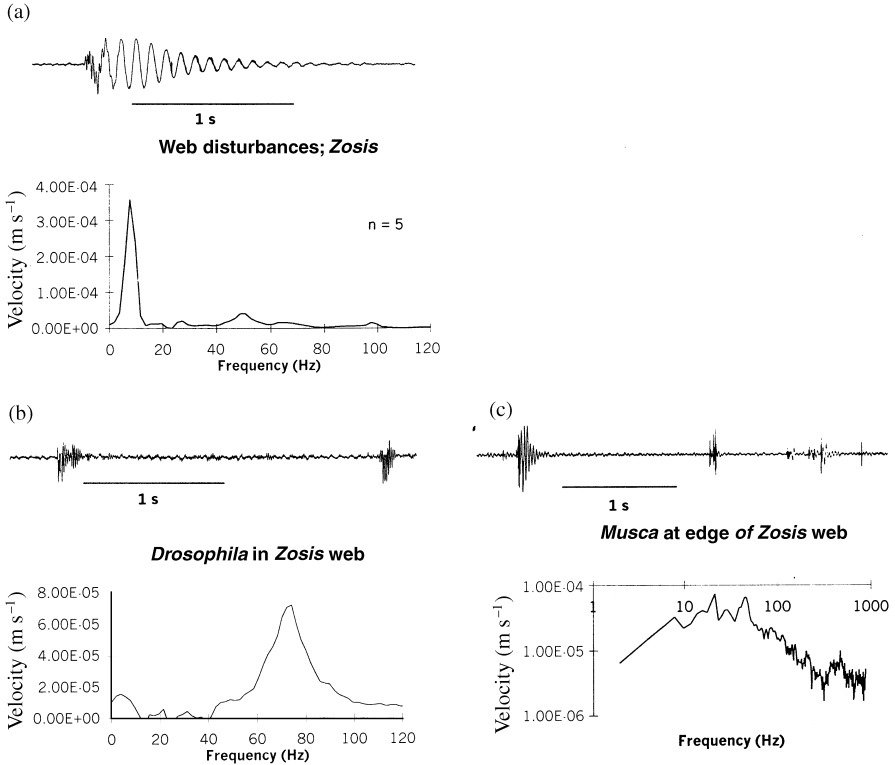


Fig. 4: Results of *Zosis*. (a) Top: signals created by 'whole-web' disturbances (i.e. knocking on the outside of the cage by dropping a 50-g weight on top of the cage); bottom: average spectrum of these signals. (b) Top: signals made by *Drosophila* caught in the web's sticky spiral; bottom: average spectrum. (c) Top: signals made by *Musca* brushing up against the web's anchor strands; bottom: average spectrum (the ordinate gives logged values)

focused on the web. Furthermore, *Zosis* reacted to *Drosophila* signals much too quickly to obtain a reading of the prey signal before *Zosis* ruined the focus of the laser. We attempted to quell *Zosis*' aggression by feeding it until it was satiated. However, this did not work: if *Zosis* was not interested in feeding, it would simply capture the prey, wrap it, and leave it hanging, presumably for later consumption. This meant that it was impossible to record prey signals with *Zosis* in the web.

Therefore, to record *Drosophila*'s signals, we removed *Zosis* from its web before adding the fly. For the purpose of recording prey signals, an intact web is essential. However, when placing a weight in the web, damage may be done to the web that may not be seen, but would nevertheless change the web's signal transmission properties (Graeser 1973; Barth 1982). Substituting the weight of the removed spider with a hanging object of the same weight was, due to the delicacy of the web, not possible without damaging the web and thereby distorting its frequency transmission properties even more dramatically than by removing the

spider. Therefore it was deemed better to remove the spider from the web (and distort the signal through the spider not being there) than to try to place a weight in the web and perhaps damage the web and distort the signal even more. More importantly, a spider hanging from its web only contacts the web through the tips of its legs; any weight we would add to the web to substitute for the weight of the spider would contact the web along a broad surface. It is known that weights hanging in the web of a spider set up unwanted resonances, and so such a weight would probably distort the signal even further. The frequency spectra of the signal produced by a *Drosophila* in a *Zosis* web with *Zosis* removed showed a single peak amplitude at around 75 Hz (Fig. 4b).

The frequency spectra of the signal made by a fly brushing up against the anchor stands of *Zosis*' web showed peak amplitudes between 400 and 500 Hz and again at around 35 Hz. However, the signal also contained a broad band of frequencies with diminishing amplitudes (i.e. 'pink noise') between 40 and 400 Hz (Fig. 4c).

Signals Made by *P. fimbriata*

As mentioned in the 'Introduction', *P. fimbriata*'s signal-generating behaviours can be categorized into three basic modes, depending upon how *P. fimbriata* manipulates the silk: (1) steady, strong silk manipulation; (2) intermittent, faint silk manipulation; (3) brief, strong rocking on the web. Each of the three modes of signal-generating behaviour used by *P. fimbriata* produced a different type of signal.

(1) Steady, strong silk manipulation. This mode of signal-generating behaviour produced signals whose frequency spectra peaked at between 10 and 20 Hz and between 45 and 75 Hz (Fig. 5b). The frequencies between 10 and 20 Hz had the greater amplitude. Usually *P. fimbriata* used this mode of signal-generating behaviour by reaching into the web so that its first pair of legs was on the sticky spiral while its rear legs remained on the wood of the cage at the web's periphery.

(2) Intermittent, faint silk manipulation. When performed from the periphery of *Zygiella*'s web, this mode of signal production generated a faint, sporadic clicking signal with peak amplitudes at around 300, 500 and 800 Hz, similar to those generated by *Drosophila* at the periphery of *Zygiella*'s web. In *Zosis*' web, these behaviours produced signals similar to those created by *Musca* brushing up against the anchor strands of the web. The signal produced spectra with a amplitude peak at 45 Hz, followed by a broad band of frequencies (i.e. 'coloured' white noise) of approximately equal amplitudes between 45 and 150 Hz (Fig. 5c). After 150 Hz, the amplitudes of the frequencies dropped off significantly, only to peak again between 400 and 500 Hz (Fig. 5d).

(3) Brief, strong rocking on the web. These behaviours produced large amplitude vibrations with frequencies principally between 10 and 20 Hz (Fig. 5a), nearly identical to those vibrations made by dropping a 50-g weight on the centre of the top of the cage. In about 10% of the instances in which *P. fimbriata* used this behaviour mode, it also took a single short step forward (toward the resident *Zygiella* or *Zosis*) at the same time as it rocked the web.

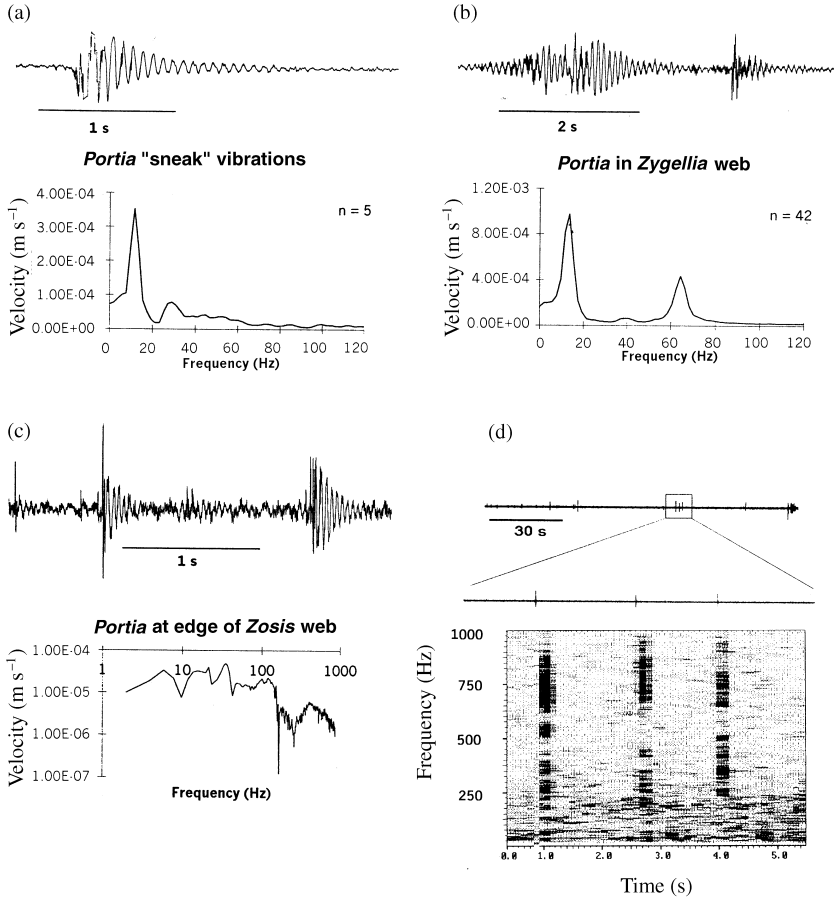


Fig. 5: Results for *Portia*. (a) Top: signal created by *Portia* making large, sudden vibrations of the web; bottom: average spectrum. (b) Top: signal created by *Portia* making large, sustained vibrations in the sticky spiral of *Zyggellia*'s web; bottom: average spectrum. (c) Top: signal created by *Portia* pulling on or brushing the anchor strands of *Zosis*' web; bottom: average spectrum (the ordinate gives logged values). (d) Top: signal created by *Portia* pulling on or brushing the anchor strands of *Zyggellia*'s web; bottom: sonagram of these signals

Circumstances under which *P. fimbriata* Adopts Different Modes of Signal-Generating Behaviour

At the beginning of tests, *P. fimbriata* walked slowly out of the tube and into the cage. Once in the cage, there was a period during which *P. fimbriata* alternated between slowly walking short distances, grooming, remaining quiescent and scanning. Scanning is a distinctive behaviour which has been described in detail elsewhere (Tarsitano & Jackson 1997; Tarsitano & Andrew 1999) in which *P. fimbriata* brings its large antero-medial eyes to bear successively on different objects in the environment. During this period, *P. fimbriata* fixated its gaze one or more times

on the lure. Over a period of several minutes, scanning became less common and walking more common. *P. fimbriata* eventually walked up a side of the cage and reached a position where the web joined the side of the cage. From here, *P. fimbriata* walked out into the web and slowly stepped out onto the silk.

P. fimbriata's first signal was generally made before going very far into the web. In about 50% of the tests, this was while *P. fimbriata*'s first pair of legs were on silk and its rear legs were still on the side of the cage. In the remainder of the tests, *P. fimbriata*'s first signal was made after all legs were on silk, but when it had gone no more than about 20 mm from the edge of the web.

P. fimbriata used two types of initial behaviour mode (see above): (1) steady, strong silk manipulation and (2) intermittent, faint silk manipulation. Which of these two behaviours *P. fimbriata* used depended on the size of the lure; *P. fimbriata* tested with small *Zosis* more often adopted the first and *P. fimbriata* tested large *Zosis* more often adopted the second [Table 1; χ^2 -test of independence (Yate's correction), $\chi^2 = 12.82$, $p < 0.001$, $df = 1$].

While within the web and near to the lure, *P. fimbriata* changed the mode of signal-generating behaviour it used. Regardless of whether it was tested with a small or a large lure, *P. fimbriata* tended more often to use strong rocking of the web while within the web and steady, strong silk manipulation or intermittent, faint silk manipulation while at the edge of the web (Table 1, large *Zosis*, χ^2 -test of independence, $\chi^2 = 46.32$, $df = 2$, $p < 0.001$; small *Zosis*, χ^2 -test of independence, $\chi^2 = 35.32$, $p < 0.001$, $df = 2$). Which behaviour *P. fimbriata* used when close to the lure was not dependent on the behaviour it used when first entering the web (Table 1, χ^2 -test of independence, ns, $df = 1$).

Table 1: Mode of signalling behaviour used by *Portia* when tested with *Zosis* lure. (a) Mode of signalling behaviour *Portia* used when first entering the web. (b) Mode of signalling behaviour *Portia* uses when close to the lure

(a)					
	Mode 1	Mode 2	Mode 3		
Small <i>Zosis</i>	21	19	0		
Large <i>Zosis</i>	5	35	0		
(b)					
	Mode 1	Mode 2	Mode 3	NS	NA
Small <i>Zosis</i>	0	9	13	3	15
Large <i>Zosis</i>	0	4	18	4	14

Mode 1: strong silk manipulation; mode 2: intermittent silk manipulation; mode 3: large-scale disturbances; NS: no signal made; NA: question of what signal made not applicable because *Portia* did not attempt to approach *Zosis*.

Discussion

Orb-web spiders have three basic types of reaction to *P. fimbriata*'s web signals. They either attack *P. fimbriata*, perform investigative behaviour (i.e. 'probing'), or ignore it as it walks across the web toward them. Corresponding to these three types of reaction to *P. fimbriata*, *P. fimbriata* has three different modes for producing signals. The first is a steady, strong silk manipulation, whereby *P. fimbriata* makes sustained (> 1 s) up-and-down movements of its palps, legs or both. The second is an intermittent, faint silk manipulation, whereby *P. fimbriata* moves one or more of its palps or legs briefly (< 1 s) and intermittently. The third is a brief, strong rocking of the web, brought about by *P. fimbriata* suddenly and rapidly flexing most or all of its legs at high amplitude, causing its body to rock violently in the web for about 1 s. It has been hypothesized that each of these modes of signal generation mimics a different type of signal; the first mode imitating prey caught in the web (Jackson 1986, 1995; Jackson & Blest 1982a; Jackson & Hallas 1986a, b), the second mode imitating faint, ambiguous prey signals from the periphery of the web (Jackson 1995; Jackson & Hallas 1986a,b), and the third mode imitating the disturbances in a web that the web spider would normally ignore (Wilcox & Jackson 1996, 1998).

As hypothesized, we found that each of these different modes of signal generation generated a different type of signal. Furthermore, we found that each of these different modes of signal generation produced a signal the average frequency spectrum of which matched the average frequency spectrum of a specific type of model signal. The waveform of the signal generated by the first mode of signal generation produced an average frequency spectrum that matched that of a fly struggling in a web. The waveform of the signal generated by the second mode of signal generation produced an average frequency spectrum that matched that of a fly at the periphery of the web brushing up against the web's anchor strands. The waveform of the signal generated by the third mode of signal generation produced an average frequency spectrum that matched that of a large-scale disturbance (i.e. the 50-g weight being dropped on the top of the cage).

What differences there are in the spectra (e.g. the second peak in the spectrum of *Musca* in *Zygiella*'s web is at 52 Hz, and the peak of *P. fimbriata*'s signalling in *Zygiella*'s sticky spiral is at 64 Hz) are probably irrelevant to *Zygiella*'s decision to treat the signal as coming from prey. Both physiological and behavioural evidence supports this conclusion. Walcott (1963) states that *Achaearanea* either cannot detect differences in the frequencies of the signals produced by bees and house flies caught in its web (although the spectra produced by these animals are different) or, if it can do so, makes no obvious use of this information. For *Zygiella* itself, Liesenfeld (1961) found that vibratory receptors had similar amplitude sensitivities when stimulated with vibrations whose frequencies were within 5–80 Hz. Barth's (1982) finding that the spider's vibratory sense organs (the trichobothria and vibration sensitive slit sensilla) are not finely tuned corroborates Liesenfeld's work, and suggests that spiders can only make crude discriminations between large frequency ranges. Therefore, in the experiments presented here, while differences

between 10, 50 and 300 Hz might well be perceived, the difference between 52 and 64 Hz probably is not.

This is the first study to examine the actual signals produced by *P. fimbriata* when using different modes of behaviour, and the first to demonstrate that *Portia*'s different modes of behaviour generate different signals with specific model signals. We demonstrate for the first time that *P. fimbriata* is in fact using a repertoire of aggressive-mimicry signals. Although we could not record the signals made by *P. fimbriata* when making sustained vibrations in *Zosis*' sticky spiral, it seems likely that these signals also imitated the signals made by prey caught in its sticky spiral. There are two reasons for believing this. First, *P. fimbriata* used mode 1 vibration-generating behaviour to generate these signals and, secondly, *Zosis* reacted to the vibrations *P. fimbriata* thereby created with a predatory attack. The same behaviour imitated prey signals in *Zygiella*'s web, so it seems likely that these signals imitated prey in *Zosis*' web as well.

Using different sizes of lures made from dead *Zosis*, we investigated the decisions made by *P. fimbriata* independent of prey reaction to the predator's behaviour. The results from these tests showed that *P. fimbriata* does not haphazardly choose modes of signal-generating behaviour. Instead, a conditional strategy seems to be adopted. *P. fimbriata* preys on other spiders which themselves are predators, and *P. fimbriata*'s conditional strategy during encounters with spiders in orb webs probably functions to minimize the risk of becoming the other spider's prey. One part of the conditional strategy appears to be: when close to the resident spider, regardless of its size, advance in conjunction with self-made smokescreen signalling. Masking its footsteps with these smokescreen signals probably minimizes the likelihood that the resident spider might flee or, what may be worse for *P. fimbriata*, make a predatory attack. When completely in the web and close to the resident spider, *P. fimbriata* would appear to be particularly vulnerable, and from this location prey-simulation signalling may be especially risky. Another part of *P. fimbriata*'s conditional strategy appears to be: when first encountering the web, make different signals depending on resident spider size (prey-simulation if the resident is small and relatively harmless; faint, ambiguous signals if the resident is large and relatively dangerous). The advantage of prey-simulation signals may be that they may facilitate rapid prey capture by quickly drawing the resident spider down into range for *P. fimbriata* to attack. However, a rapidly approaching spider may be harder to control and, if large and powerful, excessively dangerous. With faint, ambiguous signals, *P. fimbriata* avoids provoking a full-scale predatory attack and instead seems to opt for attempting a greater level of fine control over the behaviour of the resident, but with the trade-off of a longer predatory session.

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