Cyclosa turbinata (Araneae, Araneidae): Prey Discrimination via Web-borne Vibrations

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Summary. 1. The spider orb web is a structure that both restrains prey animals and carries prey-generated signals to the spider. If spiders are to discriminate among prey items without risking movement in the open and contact with potentially dangerous prey, they must be capable of interpreting web-borne vibrational signals appropriately.

2. To assess this ability in one araneid, the behavior of captive *Cyclosa turbinata* females as they preyed on five insect species was filmed under laboratory conditions. Analysis of the films showed that the movements associated with the spider's approach to live prey items varied quantitatively with prey type (Tables 1–4).

3. The vibrations induced on the web by each of the prey species were recorded on magnetic tape and analyzed with respect to absolute amplitude, amplitude modulation, and frequency components. A comparison of *C. turbinata*'s approach behavior with prey-typical vibrational differences revealed significant positive correlations (Figs. 1 and 3) and established a clear connection between the properties of web-borne vibrations and the behaviors elicited by them.

4. An evaluation of the distinctiveness of the vibrations produced by each of the five prey species revealed considerable variability within species and broad areas of overlap between species (Fig. 4). This indicated that accurate prey discrimination by appropriate interpretation of web-borne vibrations is probably not possible on *C. turbinata* webs.

Introduction

The evolution of the orb-shaped webs of araneid spiders has received considerable attention, particularly from the viewpoint of maximization of capture area within the constraints of web visibility, mass, caloric content, and resistance

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to tearing (Kaston, 1964; Langer, 1969; Eberhard, 1972; Wainwright et al., 1976). However, few authors have concerned themselves with the capabilities of the orb web as a channel across which vibrations are transmitted (Peters, 1933; Liesenfeld, 1956; Frings and Frings, 1966; Robinson and Olazarri, 1971; Finck, 1972; Witt, 1975), and none has addressed the possibility that the evolution of the araneid orb web may have occurred under information transmission constraints (Kullmann, 1972).

Whatever their evolutionary history, orb webs undoubtedly act as carriers of vibrational information during courtship (Bristowe, 1958; Platnick, 1971), predation, and predator evasion (Turnbull, 1973, and references therein). Furthermore, olfaction, vision, and audition appear unimportant in eliciting prey-capture sequences in orb-building spiders, whereas predation is regularly elicited by prey-generated vibrations transmitted by the webs (Turnbull, 1960; Frings and Frings, 1966; Walcott, 1969; Seyfarth and Barth, 1972).

The properties of those prey-generated vibrations that trigger predatory behavior in araneids have not been well studied (Liesenfeld, 1956), and suggestions by Robinson (1969) and Robinson and Olazarri (1971) that differences in vibrations may modify the spiders' predatory behaviors have apparently not been pursued. Thus, no studies have been published attempting to give a detailed interpretation of a single araneid spider's predatory behavior in the context of prey-generated signals that are transmitted on the web.

Materials and Methods

The Predator

Cyclosa turbinata Walckenaer is a small North American araneid (females reach 6 mm in length) that typically builds its orb web in forests and along forest edges. Males of the species are difficult to find and consequently were not used in this study. The webs of adult females found in late summer near Bloomington, Indiana, all contain a vertical stabilmentum extending from the hub to the upper edge of the web and composed of egg masses and debris (largely carcasses of previously consumed prey). The undisturbed female rests nearly indistinguishable at the lower end of the stabilmentum.

Unlike most araneids, which rapidly leave their webs when disturbed (Hingston, 1927; Robinson and Robinson, 1970), *C. turbinata* remains at the hub after a disturbance, or turns and grasps the lower end of the stabilmentum. Thus, *C. turbinata* could be captured by cutting the stabilmentum away from the rest of the web in the field and subsequently reanchoring the stabilmentum (with the spider hanging on) to the top edge of a 30×30 cm wooden frame. Within 24 h of capture, each spider had built a full-sized web using the original stabilmentum in its original position. In no case did a spider subsequently attempt to change its web site within the laboratory, even though the spiders were not caged or otherwise constrained.

The spiders were maintained on a light-dark regime of 16 h of light (6:00 A.M. to 10:00 P.M.) and 8 h of darkness daily, in an area where temperature was relatively constant at 21° C.

Except while under study, spiders were fed a diet of one to three live *Drosophila robusta* adults per day. Webs were sprayed with a fine mist of water at irregular intervals.

The Prey

The five prey species chosen for use in this study were *Drosophila melanogaster* Meigen, *D. robusta* Sturtevant (Diptera, Drosophilidae), *Agallia novella* (Say) (Homoptera, Cicadellidae), *Halictus* sp.

(Hymenoptera, Halictidae), and *Sitotroga cerealella* (Olivier) (Lepidoptera, Gelechiidae). These species were chosen because individuals of each could be coaxed into *C. turbinata* webs under their own propulsion and because all were easily captured or cultured. Also, Drosophillids, Cicadellids, and Halictids were represented in the array of prey types encountered by spiders in the field (unpublished data). The moth, *S. cerealella*, was included in the study for two reasons: first, various authors (Eisner et al., 1964; Robinson and Robinson, 1970) have noted that butterflies and moths are well adapted for rapid escape from araneid webs, and second, Robinson and Olazarri (1971) have suggested that certain attack behaviors of one Araneid (*Argiope argentata*) may have been retained through evolution in response to that lepidopteran adaptation. Thus, the possibility that ensnared *Sitotroga cerealella* elicit lepidopteran-specific behaviors from *C. turbinata* was the reason for including the moth in the list of experimental prey.

Insect-generated Signals

Potentially, spiders could respond differentially to any of the following parameters of prey-generated vibrations: absolute amplitude, amplitude modulations or patterns, harmonic structure, and tone sequences. To assess these parameters, magnetic tape recordings were made of the vibrations produced by live prey items as they became ensnared in freshly made *Cyclosa* webs.

Two transducers were used. Low frequency vibrations, in the 0–100 Hz range, were recorded using light from a helium-neon laser (Model 155, Spectra Physics, Mountain View, California). The beam was focused on a 2×2 mm (0.2 mg) piece of magnetic tape that had been cemented with saliva to the hub of a *Cyclosa* web. The path of the laser beam was perpendicular to the plane of the web and was adjusted so that half of the focused dot (diam about 0.5 mm) passed by the mylar chip and was absorbed on the surface of a 3×4 cm selenium solar cell (#276-115, Radio Shack, Fort Worth, Texas). The output of the cell fluctuated with the movement of the shadow cast by the web-mounted flake. Amplification in this system was partly governed by dot size, and dot size varied from preparation to preparation. Thus, recordings of optically sensed vibrations were not used for amplitude measurements (see below). High frequency vibrations, in the 60–1000 Hz range, were transduced with a crystal phonograph cartridge to which a 4 cm length of nichrome wire had been soldered, thus extending the effective length of the needle. The spring constant of this probe, measured at the tip, was approx. 1900 dynes/cm. The end of the probe was cemented with hot wax to the hub of a web and the output recorded as described above. Both transducers were sensitive to vibrations smaller than 1 µm in amplitude.

Absolute amplitudes of prey-generated signals could not be measured directly, but since all recordings of such signals were made under standardized conditions and with a fixed amplification (using the crystal probe), the amplitude of the analog signal recorded on magnetic tape could be used as an index of absolute amplitude. The relative amplitude of a prey-generated vibration was obtained by measuring the maximum peak-to-peak amplitude occurring during the first 50 ms of the recorded signal as displayed on a storage oscilloscope.

Patterns of signal amplitude were more difficult to quantify. Analog recordings on magnetic tape were digitized by a PDP-12 (Digital Equipment Corporation, Maynard, Mass.) computer at a sampling rate of 1000 samples per second and further analyzed in digital form.

A signal-amplitude profile was generated for each impact of a prey insect. The profile was formed by dividing the first second of signal after initial impact into intervals, then summing the absolute values of the amplitudes within each interval. These sums were plotted against time to give a visual impression of the vibrational energy distribution within the first second of web ensnarement.

Power spectra were generated for each prey species using the PDP-12 computer and the digitized versions of recordings of web-borne vibrations described above. The computational method involved Fourier analysis of one second of digitized data, beginning with the prey's initial impact on the web. With this method, described fully by Bendat and Piersol (1971), a power spectrum was generated for several individual impacts of each of the five prey species. A characteristic power spectrum for each species could then be derived by summing each frequency band across all impacts for one prey type, averaging them, and plotting the means against frequency. In all low-frequency power spectra, the 60-Hz peaks were eliminated to make the plots more readable. Statistical analyses of the spectra were not attempted.

Predatory behavior sequences were elicited from eight *C. turbinata* females by allowing individual prey to fly or hop into the spider's webs. The sequences were filmed at 18 frames per second (fps) using a Honeywell Elmo super-8 movie camera placed 30 cm from the web. The camera was switched on before an insect flew into the web and was not turned off until the spider had touched the prey. For both qualitative and quantitative analysis of *C. turbinata*'s behavior, the filmed sequences were viewed at 6 fps and each unit of behavior timed with a stopwatch. Intensity differences in specific behavioral units (e.g.. degree of foreleg flexion during a 'pause-en-route') were not recorded.

Preliminary observations indicated that the predatory behavior of *C. turbinata* females was different depending on whether they were actively feeding at the time of prey presentation. Consequently, to limit the variance of approach parameters, behaviors of feeding spiders were analyzed separately from those of nonfeeding spiders.

For timing purposes, each behavioral sequence was divided into three sections as follows: from the impact of prey until the spider began to move, from the beginning of the first motion to the spider's departure from the hub, and from departure to contact with the prey. The duration of a delay of approach was calculated as the sum of the first two sections. In calculating the rate of approach, the third section could not be used without modification, since that time included pauses-en-route (see below). Instead, the duration of each such pause (when it was >0.2 s and could be measured accurately) was subtracted from the third section (above), and the difference used in rate calculations.

Results

Description of Behaviors

C. turbinata awaits prey while hanging with cephalothorax downward at the hub of the web. The tarsal claws of all eight legs are in contact with spiral threads of the hub mesh immediately ventral to the spider. Any change in a spider's posture or position occurring after prey impact but before the spider had left the hub was considered monitoring.

Two types of monitoring were observed. In one type, the spider rotated very rapidly around the hub to face in the direction of the prey. (This movement is indistinguishable from the rotation preceding an approach to prey in cases when the spider does no monitoring.) While facing the prey, the spider either flexed legs I in unison so slowly that there was no visible jerk ('turn-and-pull'), or rapidly jerked the web with legs I and II hard enough to cause the prey to move visibly ('turn-and-jerk'). A simple turn with no following leg flexion is referred to as a 'turn-toward-prey'.

The second type of monitoring, which occurred only when the spider was feeding, involved a single leg. One of either the first or second pair of legs was extended toward the prey and grasped a radius running toward it ('one-leg-monitor'). The leg was either subsequently withdrawn or the spider rotated and approached the prey, sometimes after as much as several minutes.

Upon leaving the hub, the spider made either an uninterrupted approach to the prey, or one interrupted by 'pauses-en-route' (see below). In both cases the movement was rapid (averaging about 2.5 cm/s). Timing began with departure from the hub and ended with initial contact with prey.

A pause-en-route consisted of a pause in the approach, during which the

Table 1. Latency of the first motion made by a female *Cyclosa turbinata* after the impact of an insect on the web. Analysis of variance on data from nonfeeding spiders indicates that differences cannot be attributed to chance ($P < 0.05$, $F = 3.14$). By the same test, differences in data from feeding spiders could have occurred by chance

Prey species	Mean duration (s ± 1 SE)	
	Spiders not feeding	Spiders feeding
Agallia novella	0.0 ± 0.04 (10)	0.2 ± 0.09 (17)
Drosophila robusta	0.5 ± 0.23 (14)	0.4 ± 0.21 (24)
Halictus sp.	0 (17)	
Sitotroga cerealella	0.1 ± 0.06 (16)	0.5 ± 0.17 (11)

Table 2. Frequency of turn-toward-prey as the first motion of *C. turbinata* after prey impact on the web. Turn-toward-prey was the most common first motion. Others were turn-and-pull, turn-and-jerk, and one-leg-monitor. Each of these behaviors is described in the text. Asterisks indicate that *S. cerealella* and *D. robusta* frequencies were significantly different from one another ($\chi^2 = 4.65$, $P < 0.05$). Other pairwise comparisons revealed no significant differences

Prey species	Frequency of turn-toward-prey	
	Spiders not feeding	Spiders feeding
Agallia novella	60% (10)	41% (17)
Halictus sp.	88% (17)	
Sitotroga cerealella	56% (16)	9% (11)*
Drosophila robusta	57% (14)	54% (24)*

spider sharply flexed legs I and II in unison. The jerk caused by this flexion was not obviously different from that produced during the turn-and-jerk, and thus the latter, as a distinct behavioral unit, may be only an artifact of the timing procedure.

Behavior as a Function of Prey Type

D. melanogaster, *D. robusta*, *A. novella*, *Halictus* sp., and *S. cerealella*, when ensnared, elicit quantitatively different behaviors from the spiders. These differences are detailed in Tables 1–4. *D. melanogaster* data appear only in Table 4 since this insect was used only during preliminary work, during which not all parameters of approach behavior were recorded.

Tables 1 and 2 involve elements of behavior that occurred before the spider left the web's hub, while Tables 3 and 4 concern approach behaviors. Significant

Table 3. Frequency of 0, 1, 2, 3, or 4 pauses during *Cyclosa turbinata* approaches to ensnared prey. Among nonfeeding spiders, *Halictus* sp. scores were significantly different from others pooled (2×5 table, $\chi^2 = 9.81$, $P < 0.05$). Among all spiders, *Halictus* sp. scores were also significantly different from others pooled (2×5 table, $\chi^2 = 13.7$, $P < 0.01$). The means of the number of pauses per approach to each prey species cannot be used in statistical comparisons, since the data are not normally distributed. However, the means will be used later (Fig. 3) as indices of the pause-en-route distributions

Prey species	Number of pauses per approach (Spider not feeding)					
	0	1	2	3	4	Mean number ± 1 SE
Agallia novella	5	2	3	0	0	0.80 ± 0.29
Drosophila robusta	6	5	2	1	0	0.86 ± 0.25
Halictus sp.*	3	5	7	2	0	1.47 ± 0.23
Sitotroga cerealella	11	3	1	0	1	0.56 ± 0.30

Prey species	Number of pauses per approach (All spiders)					
	0	1	2	3	4	Mean number ± 1 SE
Agallia novella	12	10	5	0	0	0.74 ± 0.15
Drosophila robusta	19	11	7	1	0	0.74 ± 0.14
Halictus sp.**	3	5	7	2	0	1.47 ± 0.23
Sitotroga cerealella	16	7	3	0	1	0.63 ± 0.19

Table 4. Rates of *Cyclosa turbinata* approaches to ensnared prey. Pauses en route to prey, when of measurable duration, were subtracted from the approach times before approach rates were calculated. Means and standard errors of prey mass were calculated on the basis of a sample of 10 from each population, not on the basis of individual weights of actual prey used in the experiments

Prey species	Mean mass (mg ± 1 SE)	Mean rate of approach (cm/s ± 1 SE)		
		Spiders not feeding	Spiders feeding	All spiders
Drosophila melanogaster	0.7 ± 0.05	1.8 ± 0.22 (12)	2.5 ± 0.21 (31)	2.3 ± 0.17 (43)
Agallia novella	0.9 ± 0.14	2.4 ± 0.23 (10)	2.3 ± 0.29 (17)	2.3 ± 0.20 (27)
Drosophila robusta	1.2 ± 0.05	2.0 ± 0.23 (14)	2.2 ± 0.18 (24)	2.1 ± 0.14 (38)
Halictus sp.	2.5 ± 0.14	2.5 ± 0.35 (17)		2.5 ± 0.35 (17)
Sitotroga cerealella	3.8 ± 0.41	2.9 ± 0.28 (16)	3.0 ± 0.55 (11)	2.9 ± 0.27 (27)

Regressions of mean rates of approach on mean prey mass:
  Spiders not feeding   slope $= 0.286$ $P < 0.05$ ($r = 0.88$, $P < 0.05$)
  All spiders   slope $= 0.213$ $P < 0.025$ ($r = 0.92$, $P < 0.05$)

differences in *C. turbinata* behavior are noted in each table. (In Table 4, an analysis of variance on the approach-rate data does not indicate that the differences are significant. However, the rates of approach are significantly related to the mean mass of the prey insects.)

The data tabulated in Tables 1–4 confirm the preliminary observation that preapproach and approach behaviors changed depending on whether or not

the spiders were actively feeding at the time of prey impact on the web. These results justify the division of spiders into two state-categories for analytical purposes.

Properties of Insect-generated Signals

The means of maximum relative amplitude that were detected during the first 50 ms of prey-generated signals were as follows: *D. melanogaster* 1.58 ± 0.24 (arbitrary units ± 1 SE) $N=10$; *D. robusta* 1.43 ± 0.29 $N=16$; *A. novella* 1.46 ± 0.23 $N=11$; *Halictus* sp. 1.90 ± 0.26 $N=11$; *S. cerealella* 2.77 ± 0.42 $N=9$. These amplitudes are significantly correlated with prey mass ($r=0.95$, $P<0.05$) and a regression of mean amplitude on mean mass yields the line amplitude $=0.45$ mass $+1.01$, with the slope significant at $P<0.025$.[1] This and the relationship between prey mass and approach rates (see Table 4), suggests that impact amplitudes should be positively correlated with approach rates. In fact, the two measures are highly correlated ($r=0.98$, $P<0.01$) and a regression of approach rate on impact amplitude yields the equation rate $=0.53$ amplitude $+1.49$ (slope significant at $P<0.005$). This relationship is shown in Figure 1.
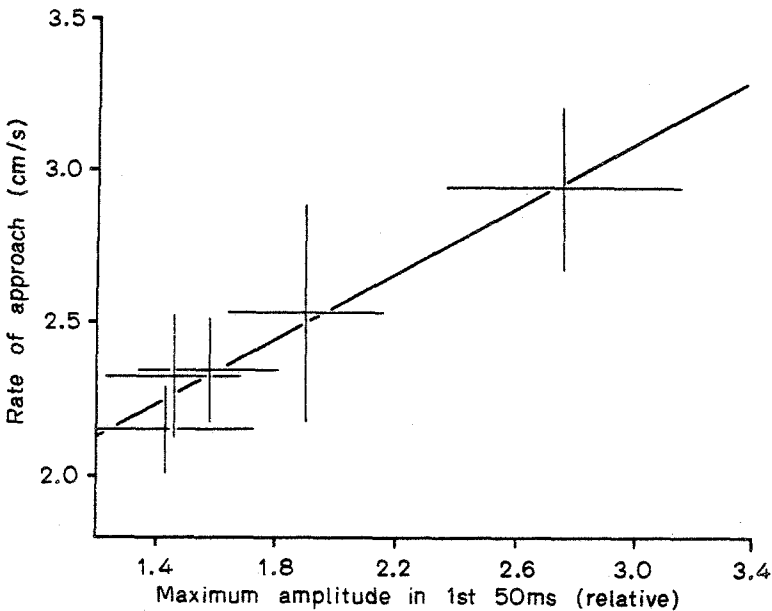

Fig. 1. The linear relationship between *C. turbinata*'s mean approach rate and the mean amplitude (at impact) of prey-generated vibrations. Mean approach rates and mean amplitudes are shown ± 1 SE. The slope of the regression line is significant ($P<0.005$). From left to right, prey represented are *Drosophila robusta, Agallia novella, D. melanogaster, Halictus* sp., and *Sitotroga cerealella*

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[1]   In all comparisons of an approach variable with a measurable characteristic of each prey type, only mean values of both dependent and independent variables could be used, since at the time of filming of approach behavior, no measurements of prey parameters other than by species were made
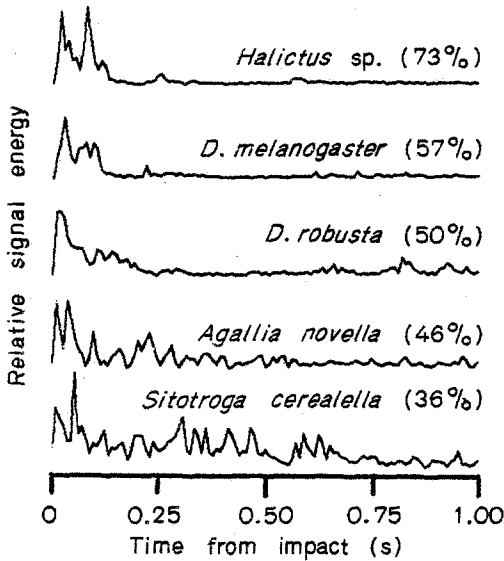
Fig. 2. Examples of the energy distribution of prey-generated vibrations transmitted along radii of *Cyclosa turbinata* webs. Each profile depicts the pattern of energy distribution that is typical for the prey species represented. Percentages to the right of each profile indicate the mean proportion of the energy concentrated in the first quarter-second. Analysis of variance on these proportions indicates that differences cannot be attributed to chance ($P < 0.005$, $F = 11.83$)
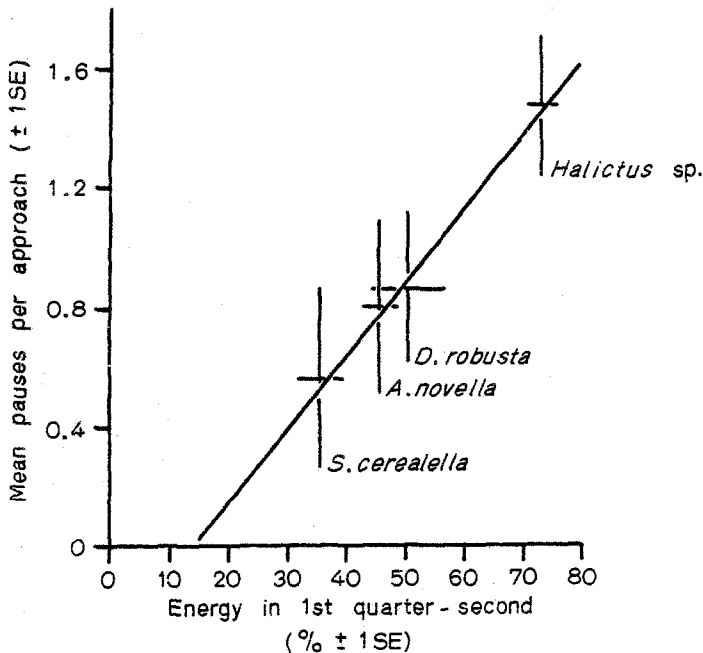

Fig. 3. The linear relationship between *C. turbinata's* mean number of pauses per approach (Table 3) and the proportion of web-borne energy contained in the first quarter-second after prey impact (Fig. 2). The mean number of pauses per approach and the mean energy proportions are shown ± 1 SE. The slope of the regression line is significant ($P < 0.005$)
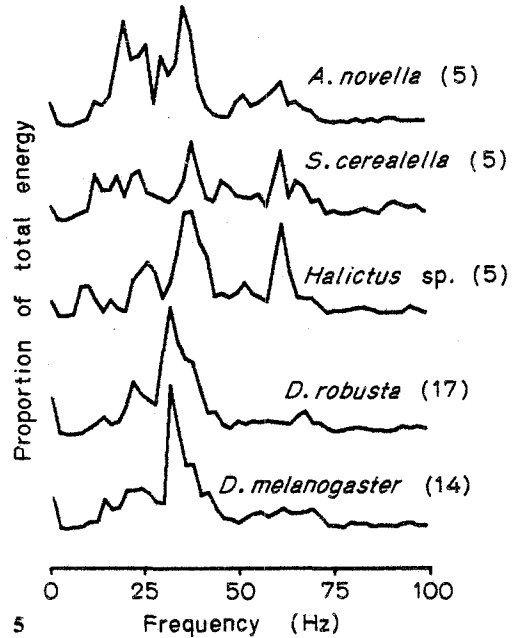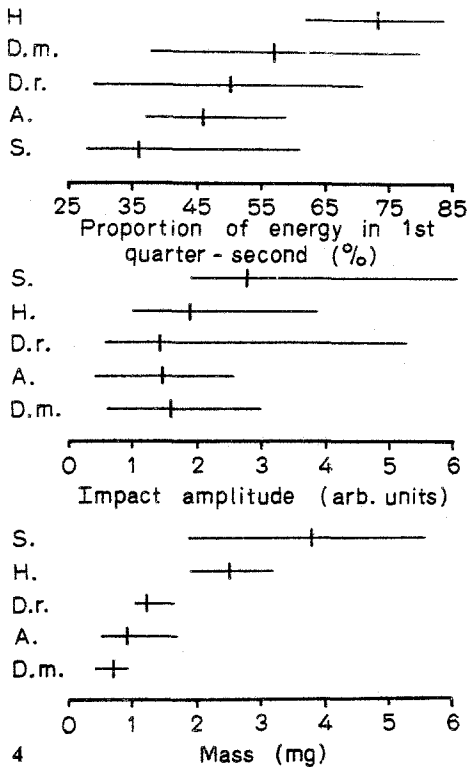
Fig. 4. The means (*vertical lines*) and ranges (*horizontal lines*) of three of the vibration and prey parameters that significantly affect *C. turbinata's* behavior. Explanation of abbreviations: *H.*, *Halictus* sp.; *D.m.*, *Drosophila melanogaster*; *D.r.*, *Drosophila robusta*; *A.*, *Agallia novella*; *S.*, *Sitotroga cerealella*

Fig. 5. Averaged power spectra showing the distribution of lower frequencies in the web-borne vibrations produced by each prey species. The number to the right of each spectrum indicates the sample size

Figure 2 shows a sample energy profile (the one whose energy distribution best matches the mean profile for the species it represents) for each of the five prey species. The percentage to the right of each profile indicates the mean proportion of the energy concentrated in the first quartersecond and provides a quantitative index of energy distribution. This index is positively correlated with the number of pauses per approach (Table 3) by nonfeeding spiders ($r=0.99$, $P<0.01$). A regression (Fig. 3) of pauses per approach on the proportion of energy in the first quartersecond yields the line pauses $=0.024$ energy -0.33, with the slope significant at $P<0.005$. The ranges of mass, impact amplitude, and struggle pattern for each prey species are shown in Figure 4.

Figures 5 and 6 show, for each prey species, characteristic power spectra in the low and high frequency ranges, respectively. Since no statistical tests were made on the spectra, Figure 7 is included to show the variation among the spectra from which the averaged power spectrum for *A. novella* was derived.
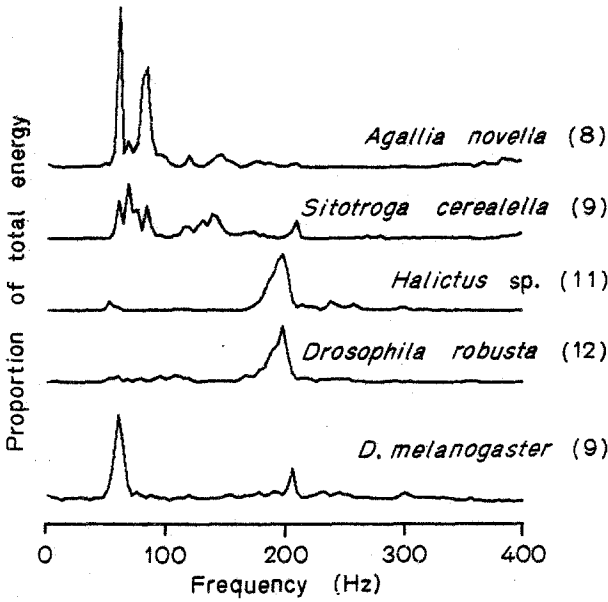
Fig. 6. Averaged power spectra showing the distribution of higher frequencies in the web-borne vibrations produced by each prey species. The number to the right of each spectrum indicates the sample size
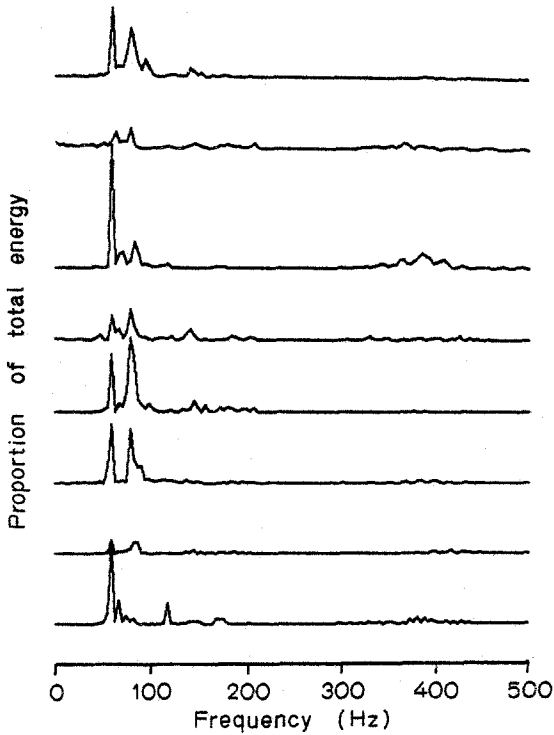

Fig. 7. Individual power spectra of vibrations produced by *Agallia novella*. These spectra are presented to illustrate the amount of variability in the power spectra of a single species

Because power spectra covering the full 60–1000 Hz range revealed no insect-generated vibrational energy above 400 Hz, the higher frequencies are not included in Figures 6 and 7. In the same figures, the high peaks at 60 Hz are attributable to line interference and should be ignored.

Discussion

Signal Correlates in Behavior

Several authors have noted that orb-weaving spiders alter their behavior in characteristic ways when presented with different prey types (see, for example, Robinson and Olazarri, 1971; Robinson and Mirick, 1971; and Harwood, 1974). However, most of these prey-dependent changes occur after tactile contact has been made with the prey item, and consequently cannot necessarily be attributed to differences in web-transmitted signals. Only Robinson and Mirick have alluded to a spider's (*Nephila clavipes*) tendency to approach different prey items at characteristically different speeds and with characteristically different postures.

The behavioral data in Tables 1 – 4 indicate that *Cyclosa turbinata* is another araneid that perceives differences among prey types on the basis of web-borne information.

In two instances, vibrational differences eliciting changes in behavior have been identified. The relationship between rate of approach and impact amplitude (Fig. 1) is interesting in view of the contrasting results obtained with a large tropical araneid, *Nephila clavipes*. Robinson and Mirick (1971) noted that this spider characteristically approaches very large or very heavy insects more slowly than it does smaller ones, and with a distinctive posture. It may be that *Cyclosa*, too, would approach prey much larger than *S. cerealella* more slowly, reflecting a conflict between approach and retreat tendencies. The possibility that *C. turbinata* could infer prey mass from the resonant motion of prey in the web, rather than from impact amplitude, can be discounted (Suter, in preparation).

The relationship between the energy profiles of the five prey species' web vibrations and the spider's pauses-en-route (Fig. 3) suggests that each pause constitutes a brief interval of few spider-generated vibrations during which the spider can confirm the continued presence of prey in the web. This interpretation follows from two observations. First, a pause with flexion of legs I and II always occurred when a prey item escaped from the web before the spider had reached it. Second, the individual energy profiles that the data in Figure 2 represent reveal that the first quartersecond energy figures provide an accurate inverse measure of how often, during the first second, no prey-generated vibrations were detectable on recordings.

Cyclosa's uninterrupted approach to continously vibrating prey (e.g. *S. cerealella*) and its pause-punctuated approach to intermittently vibrating prey (e.g., *Halictus* sp.), imply that the spider is able to sense prey-generated vibrations while in motion and producing its own high-amplitude vibrations. This ability to resist jamming by its own vibrations has not previously been noted in the literature on arthropod orientation to prey (Rudolph, 1967; Markl and Wiese,

1969; Murphey, 1971). Furthermore, the contrasting struggle patterns of *S. cerealella* and *Halictus* sp. reflect activity patterns that may be adaptive for ensnared prey. For example, *Sitotroga*'s struggles are more evenly distributed during the first second of contact with the web than are the struggles of any other of the tested species; and for a species whose contact with a sticky web is tenuous (Eisner et al., 1964), this continued struggle may facilitate escape. *Halictus*, however, behaves more like debris, hitting the web and subsequently struggling very little. Visual observation of *Halictus* behavior while in the web reveals that the bee does not beat its wings until both have been freed of viscid spiral threads by cleaning motions of the legs. In contrast, enmeshed *Sitotroga* beats its wings without fully extending them, and while keeping its legs close to thorax and abdomen. These moth movements, being quite different from normal flight movements, suggest specific web-escape behavior.

Bases for Pretactile Prey Discrimination

The view that animals select an energetically, temporally, or nutritionally optimal diet from among the many diets available to them has recently received theoretical backing as well as limited empirical confirmation (Emlen, 1966, 1968; Schoener, 1971; Emlen and Emlen, 1975; Ellis et al., 1976). The central assumption in the theory of feeding strategies is that the efficiency with which an animal obtains food affects that animal's fitness and consequently should be maximized through natural selection.

   In that context, the approach to an ensnared but inedible insect and the subsequent attack on it may constitute significant energetic costs to the spider, costs which would be avoided if it could learn to discriminate inedible from edible prey. If the 'principle of allocation' (Levins and MacArthur, unpublished) is valid, then such a reduction in pursuit costs would allow an increase in reproductive effort, presumably increasing fitness. In addition, a spider's approaches to inedible prey items increase the probability that the spider will be consumed, and the elimination of such approaches should enhance the spider's fitness by decreasing adult mortality.

   Thus at least two selective forces, each favoring the use of some sense modality in the discrimination of prey type, probably act on araneids. Whether these selective forces are sufficient to foster evolutionary development of an ability to discriminate among vibration depends, in part, on the species distinctiveness of these web-borne vibrations. Data presented in this paper indicate that ensnared and struggling prey generate web-borne vibrations which, for five species at least, are statistically typical of each species. However, the distinctiveness of these signals is slight both with respect to amplitude (Table 4, page 289, and Fig. 4) and frequency (Figs. 5 and 6). Consequently, it is unlikely that prey discrimination by appropriate interpretation of web-borne vibrations occurs in *Cyclosa*.

   This conclusion does not mean that *Cyclosa turbinata*'s responsiveness to variations in the mass and activity pattern of ensnared prey is nonfunctional. Since the caloric content of an insect is directly (though roughly) proportional

to its mass, a spider's ability to discern the relative mass of an insect endows the spider with a mechanism for evaluating the insect's relative food value. Thus, it is not surprising that *C. turbinata* approaches larger prey more rapidly. Similarly, a spider that pauses when uncertain of the presence of prey in the web is unlikely to waste calories and incur risk in pursuit of insects that have already escaped from the web. In this context, a correlation between the number of pauses-en-route to prey and the struggle pattern of the prey is easily understood.

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