THE ROYAL
SOCIETY

Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour

Takeshi Watanabe

Department of Zoology, Faculty of Science, Kyoto University, Kyoto 606–8502, Japan (takeshi@ecol.zool.kyoto-u.ac.jp)

An uloborid spider (*Octonoba sybotides*) constructs two types of web which are distinguished by linear or spiral stabilimenta. Food-deprived spiders tend to construct webs with spiral stabilimenta and food-satiated spiders tend to construct webs with linear stabilimenta. I experimentally examined the influence of web type on the speed of a spider's response to small and large flies. The results indicated that web type rather than the spiders' energetic condition influences the response speed to small or large *Drosophila* flies. I also examined whether thread tension affects the response speed of spiders by increasing the tension of the radial threads. The results showed that spiders on an expanded web responded to small prey as quickly as spiders on webs with spiral stabilimenta. The tension of the radial threads may be regulated by the degree of distortion of the radial threads at the hub. *O. sybotides* seems to construct orb webs which induce different responses for smaller, less-profitable prey according to its energetic state. The spider appears to increase the tension of the radial threads so that it can sense smaller prey better when hungry.

Keywords: vibration; information; tension; *Octonoba*; response speed

1. INTRODUCTION

The interaction between organisms and their environment, including other organisms, is a fundamental facet of animal ecology. One important interaction between organisms and their environment is the transmission of information (Dusenbery 1992). Web-spinning spiders acquire much of the information about their prey on their webs from vibrations transmitted through the web threads (Klärner & Barth 1982). Their response to prey seems to be physiologically tuned to transmitted vibrations of a specific frequency and amplitude range and spiders need to be stimulated above a threshold level to induce prey-catching behaviour (Klärner & Barth 1982; Masters 1984*b*; Landolfa & Barth 1996).

In general, small prey items of relatively little nutritional value are rarely attacked (Riechert & Luczak 1984; Uetz & Hartsock 1987) and foraging models which include diet width predict the advantage of such tactics (Charnov 1976). Prey discrimination (size or prey species) may use frequency or amplitude information (Landolfa & Barth 1996). Physiological studies on web vibrations and the vibration sense of spiders have brought us much knowledge about the sensory mechanisms which spiders use to detect prey. However, these physiological investigations usually neglect to take into account the condition of each individual spider in an ecological context. Recent studies have shown that feeding history affects the prey-capture behaviour of an orb-web spider (Herberstein *et al.* 1998). Food-deprived spiders reacted to smaller prey more often and more quickly than satiated spiders. Success in capturing prey is critically affected by the speed with which the spider arrives at its struggling prey (Riechert & Luczak 1984). Food-deprived spiders seem to target any prey, including smaller items with relatively little energetic return, while food-satiated spiders target larger prey. The unsolved question is how a spider is able to respond differently to different-sized prey.

If a spider's prey-attacking behaviour is influenced by energetic conditions (food deprived or satiated), it is usually assumed that their decision making is the result of various, complex, internal processes (nerves, hormones, etc.). However, it is also possible that the difference in a spider's response to smaller prey is externally induced by differences in the intensity of vibrations transmitted through the web threads. The vibrations generated by the same prey will be transmitted to the spiders differently if the tension of the web threads is changed. For example, the resonance frequency decreases with increased thread tension (which is dependent on the mass on the web) and a spider's response threshold also decreases slightly as the tension increases (Masters 1984*a*,*b*). Since the peak amplitude of prey-generated web vibration depends on the mass of the insect (Landolfa & Barth 1996), smaller prey which generate low amplitude vibrations may be detected more easily when the thread is under greater tension. In addition, peaks in both the longitudinal and transverse vibration spectra of small insects occur at a higher frequency range than those of larger insects (Masters 1984*b*; Landolfa & Barth 1996). Theoretically, the cut-off frequency, above which the transmission falls rapidly, is lower when the tension decreases (Masters 1984*b*). Therefore, vibrations generated by smaller insects may barely be transmitted on relatively loose threads. These findings suggest that the properties of a spider's web threads can externally affect the prey-catching behaviour of spiders.

For the reasons mentioned above, we cannot assume *a priori* that a spider's different responses are induced by a change in internal factors, since the response to smaller prey is correlated to both the spider's energetic state and changes in their web structure.

In this paper, I show that the response speed of an orb-web spider (*Octonoba sybotides* (Uloboridae)) to prey insects is regulated by web design and seems to be related to the tension of the radius threads. *Octonoba sybotides* is known to add two distinct forms of stabilimentum to the

Received 16 November 1999 *Accepted* 14 December 1999

web: linear and spiral (Watanabe 1999*a*). The two forms of stabilimentum correspond well to the energetic state of the owner spiders; food-satiated spiders tend to form linear stabilimenta and hunger induces the spiders to form spiral stabilimenta (Watanabe 1999*b*). I found that hungry spiders (on webs with spiral stabilimenta) react to smaller flies much faster than food-satiated spiders (on webs with linear stabilimenta). I hypothesized that the difference in the spiders' responses is related to the type of web, as distinguished by the form of stabilimentum added to the orb web. Webs with the spiral form of stabilimentum have radial threads under higher tension and induce the spider on the web to respond to smaller prey more quickly. To examine this hypothesis, I conducted the laboratory experiments described below.

2. METHODS

(a) *Feeding experiments*

Adult female *O. sybotides* collected in early September 1998 from the field (Botanical Garden of the Faculty of Science at Kyoto University, Kyoto, Japan) were placed in individual cylindrical cases 10 cm in diameter and 8 cm high. All of the spiders were kept in the laboratory at a constant temperature (25 °C). They made horizontal orb webs in the cases within a few days. By keeping the spiders either food satiated (two fruit flies per day) or food deprived (no flies), I could induce the spiders to add linear or spiral stabilimenta to their webs within three weeks. (For further details of the feeding regimes, see Watanabe (1999*b*).) Large (*Drosophila virilis*, 2.9–3.4 mm total length (TL) and 2.1–2.9 mg) and small (*Drosophila melanogaster*, 1.8–2.0 mm TL and 0.7–1.2 mg) fruit flies were used for the feeding experiments. I caught a fruit fly in a jar (40 mm long × 15 mm in diameter) and put it into a refrigerator for 4 min to weaken it. Then I put the fly onto the web 3 cm from the spider, at 90° from the direction the spider was facing. All of the flies attached to webs began to move their legs and wings within 15 s. The spider rapidly turned towards the struggling fly and then dashed along a single radial thread to the fly and wrapped it. Using a stopwatch, I recorded the time from the spider's initial turn until it started to dash towards the struggling prey. Although the stopwatch recorded hundredths of a second, I rounded off the time to one decimal place because the value at two decimal places seemed to be unreliable. When Herberstein *et al.* (1998) measured travelling time, they added the period measured in this study to the period between leaving the hub and reaching the prey. However, I did not include the time taken to reach the prey, since the weight of the spider seemed to affect its speed: food-satiated spiders were usually heavier and slower than food-deprived spiders. A spider never broke off its attack once it started to move towards its prey. Captured flies were immediately taken away from the spiders. I allowed an interval of 3 h between feeding trials (supplying large and small flies).

After recording four data points (large and small flies on webs with linear stabilimenta and large and small flies on webs with spiral stabilimenta) for each spider (30 individuals), I conducted replacement experiments. The same 30 spiders were randomly paired into 15 pairs and retested. A spider from a web with one type of stabilimentum was exchanged with a spider from a web with the other type of stabilimentum. After recording the prey response times, I let all the individuals construct another web with the opposite type of stabilimentum by controlling their food supply (satiated or deprived feeding treatments) and again exchanged the spiders and measured their response times to large and small prey. Since it is possible that the act of replacement might itself affect the behaviour of the spiders on the webs, I also conducted replacement experiments between webs with the same type of stabilimentum with a second set of randomly chosen pairs. As mentioned above, 30 similar spiders were assigned to the following treatments: (i) undisturbed (control 1), (ii) disturbed (control 2, translocation between webs with the same type of stabilimentum) and (iii) experimental (translocation between webs with different types of stabilimentum). The response speeds were compared using repeated-measures ANOVA.

(b) *Distortion of radial threads at the hub*

The function of the hub-radius attachments (figure 1) may be to regulate the tension of the radial threads (Robinson & Robinson 1970; Eberhard 1972), since the hub threads distort the radial threads. It has been suggested that the type of attachment increases the tension on the radius and may function to tighten loose radii (Eberhard 1972). The amount of distortion of a radius indicates the relative tension on that radius and the hub thread (Eberhard 1972). Thus, the distortion seems to indicate the tension on the radial threads indirectly. To estimate the distortion of radial threads, I magnified images of the webs 25-fold with a projector (Nikon V-12) in order to directly measure the length of the hub threads of webs from which the spiders had been removed. I divided the total thread length (d) by the straight line distance (R). The straight line distances ranged from 4 to 5 mm from the outermost hub connection to the centre of the web. Within this range, the hub threads (and spiral stabilimentum silk) traversed radial threads three or four times. I measured the d/R-value of ten threads randomly chosen from each web and calculated the average, which was used as the distortion index for the web. A value of $d/R = 1.0$ indicates that there was no distortion of the radial threads. As the degree of distortion increased, the value also increased. I compared the indices of webs made by the same spider with the linear and spiral forms of decoration ($n = 30$) to determine whether d/R differed (paired t-test).

(c) *Expansion experiments*

To examine whether an increase in radius thread tension induced a faster response to smaller prey, the tension of the radial threads was increased by widening the frame of the cases to which the webs were attached by anchor threads. For these experiments, the spiders were kept in cases with a frame which could be separated into four parts. When the spiders spun a web with the linear form of stabilimenta, I shifted the four quadrants of the frame outward 1.5–2.0 mm. Then, I measured the response speed of the spiders to large and small prey. The same spiders were used in these experiments and the feeding experiments described above.

3. RESULTS

The response times of the spiders (figure 2) differed significantly between the four feeding situations: small or large flies on webs with linear or spiral stabilimenta (one-way repeated-measures ANOVA, d.f. $= 3$, $F = 14.98$ and $p < 0.001$). The response times for three of the treatments were the same (small fly on a spiral stabilimentum web, large fly on a spiral stabilimentum web and large fly on a linear stabilimentum web). The response time of the

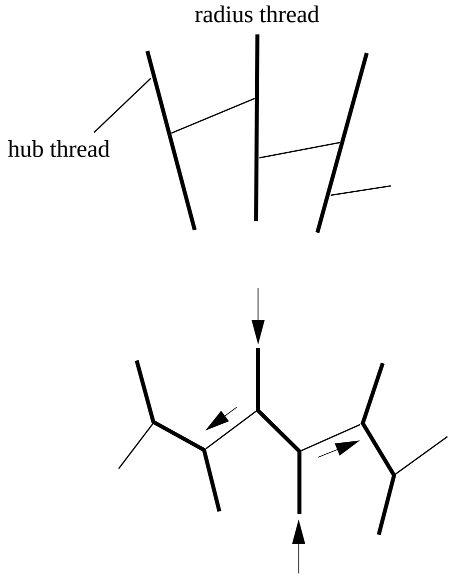

Figure 1. Attachment of hub threads to the radii. The effect of this type of attachment would be to increase the tension of the radii.

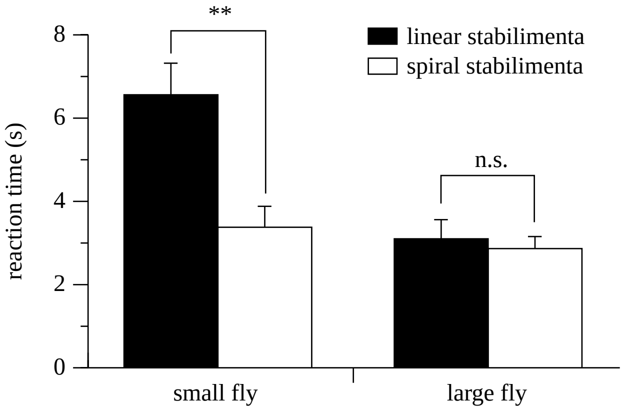

Figure 2. Mean response times of spiders ($n = 30$) on webs with linear (solid bars) and spiral stabilimenta (open bars) to small and large *Drosophila*. Error bars show the standard errors.

spiders to a small fly on a linear stabilimentum web was significantly longer than for the other three treatments (linear contrasts, all $F > 25.19$ and $p = 0.0001$).

The spiders which were moved from webs with linear stabilimenta to webs with spiral stabilimenta (experimental, linear → spiral) responded to small flies faster than those moved from webs with linear stabilimenta to webs with linear stabilimenta (control 2, linear → linear) (figure 3*a*). For larger flies, there was no difference in the reaction speeds between the two conditions. On the other hand, the spiders moved from webs with spiral stabilimenta to webs with linear stabilimenta (experimental, spiral → linear) reacted to both smaller and larger flies more slowly than those moved from webs with spiral stabilimenta to webs with spiral stabilimenta (control 2, spiral → spiral) (figure 3*b*).

The d/R-values (means ± s.d.s) of the webs with linear and spiral stabilimenta were 1.015 ± 0.006 ($n = 30$) and 1.029 ± 0.008 ($n = 30$), respectively. The degree of distortion of radial threads at the hub was significantly larger

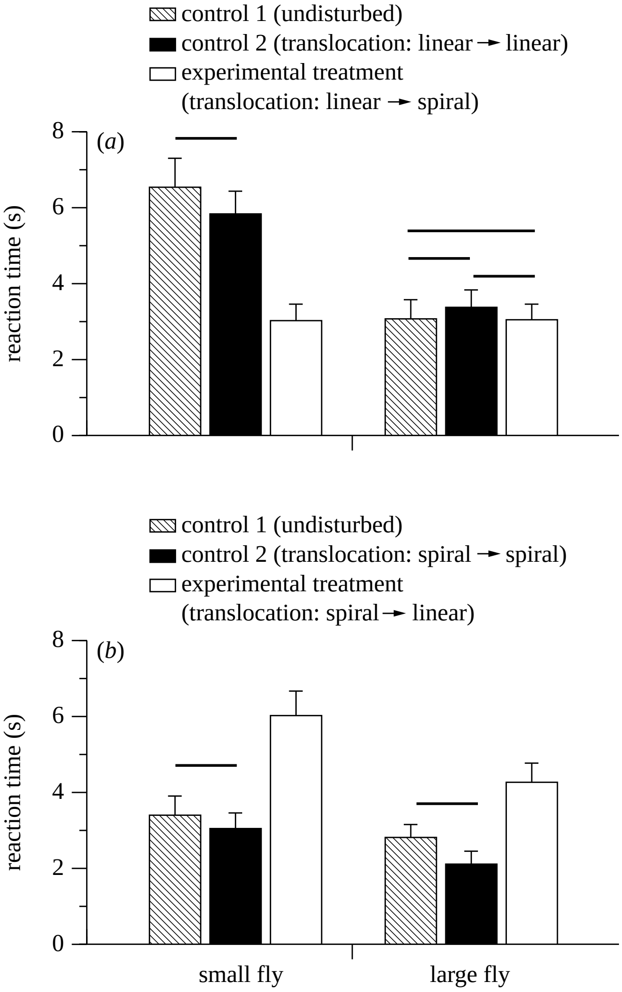

Figure 3. Mean response times of spiders in three treatments (to small and large *Drosophila*, respectively). (*a*) Experiment on spiders forming linear stabilimenta. (*b*) Experiment on spiders forming spiral stabilimenta. Undisturbed (hatched bars), translocation to a web with the same type of stabilimenta (solid bars) and experimental treatment (translocation to a web with the opposite type of stabilimenta) (open bars). The data were analysed by repeated-measures ANOVA with two within-subject factors. (*a*) Treatment ($F_{2,87} = 5.44$ and $p = 0.0069$), prey size ($F_{1,87} = 20.30$ and $p = 0.0001$) and prey size × treatment ($F_{2,87} = 6.15$ and $p = 0.0038$) were all significant. (*b*) Treatment ($F_{2,87} = 10.73$ and $p = 0.0001$) and prey size ($F_{1,87} = 5.92$ and $p = 0.0214$) were significant. Prey size × treatment ($F_{2,87} = 0.36$ and $p = 0.3622$) was not significant. Within each prey size, the horizontal lines above the bars indicate groups whose means do not differ (linear contrasts, $p > 0.05$).

on the webs with spiral stabilimenta than on the webs with linear stabilimenta (paired *t*-test, d.f. = 29, $t = 8.88$ and $p < 0.001$).

After the replacement experiment, the same 30 spiders were subjected to the expansion experiment. The spiders on expanded webs reacted to small flies significantly more quickly than the spiders on unexpanded webs. The response of the spiders on the expanded webs was as fast as the response on webs with spiral stabilimenta (figure 4). There was no statistical difference in the response speeds of the spiders to large flies.

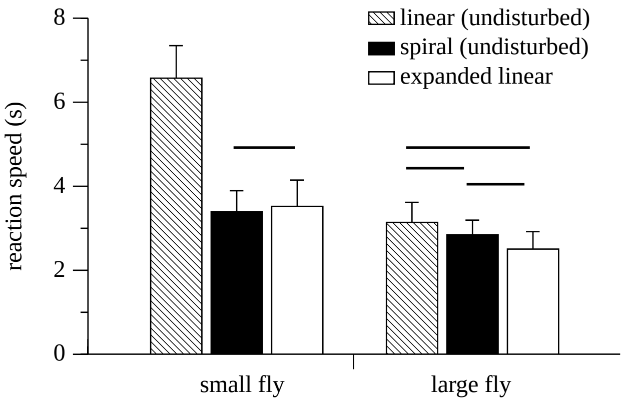

Figure 4. Mean response time of spiders for three treatments (to small and large *Drosophila*). Treatment ($F_{2,87} = 4.52$ and $p = 0.0136$), prey size ($F_{1,87} = 22.32$ and $p < 0.0001$) and prey size × treatment ($F_{2,87} = 6.67$ and $p = 0.002$) were all significant. Within each prey size, the horizontal lines above the bars indicate groups whose means do not differ (linear contrasts, $p > 0.05$).

4. DISCUSSION

This study demonstrated that a web's structure (with different types of stabilimentum) affects the response speed of a spider to prey entangled in its web. Spiders on webs with spiral stabilimenta started to dash towards small prey faster than spiders on webs with linear stabilimenta. Spiders on webs with linear stabilimenta under increased thread tension responded to smaller prey as quickly as spiders on webs with spiral stabilimenta. This suggests that the sensitivity of spiders to smaller prey increases on webs with radial threads under more tension.

A comparison of the distortion of the radial threads at the hub showed that radial threads with spiral stabilimenta were more distorted than those with linear stabilimenta. Eberhard (1972) argued that the distortion at the hub increases the tension of the radial threads and may function to tighten loose radii. However, he also argued that greater distortion of the radial threads therefore indicates that the tension of the radial threads was initially lower. The two statements may be inconsistent, because loose radii will be tightened by distortion at the hub and greater distortion may indicate higher tension on the radial threads. Therefore, his argument for the relationship between the amount of distortion and the tension of the radial threads must be reconsidered. The different interpretations of the relationship between the amount of distortion and the tension of the radial threads may occur because of a reversal of cause and effect. Hub threads may distort the radial threads to raise rather than to correct their tension.

It should be noted that central tension regulation is possible because *O. sybotides* usually constructs its web by attaching anchor threads to solid bases, such as tree trunks, logs and rocks (T. Watanabe, personal observation). If they constructed webs attached to flexible bases, such as grass stems, then central regulation of the tension of the radius threads would be impossible because the constantly shifting base would affect the tension (Wirth & Barth 1992).

In the field, the mean mesh size and catching area of webs with each type of stabilimentum differ (Watanabe 1999*a*). The mesh of webs with spiral decorations is smaller than that of webs with linear stabilimenta. On the other hand, the catching area of webs with spiral decorations is larger than that of webs with linear decorations. Although Uetz *et al.* (1978) did not find a clear positive association between mesh and prey size among species, a narrower mesh would be more effective for catching smaller flying insects (Murakami 1983; Sandoval 1994). Therefore, the enhanced sensitivity for smaller prey corresponding to the change in web structure seems to be an adaptation for catching prey when smaller prey is included as a target.

The dimorphic stabilimenta (spiral and linear) of *O. sybotides* webs may have a function related to regulating web tension. The attachment of spiral stabilimenta at the hub resembles that of hub threads and the threads of spiral stabilimenta are usually laid alongside the hub threads (T. Watanabe, personal observation). The attachment of additional spiral stabilimenta at the hub may support the distortion of the radial threads by the hub threads, although the stabilimentum silk is usually thought to be attached too loosely to have any mechanical effect on the web (Eberhard 1973).

Eberhard (1973) observed the orientation of the linear stabilimenta of *Uloborus diversus*, which constructs webs with dimorphic stabilimenta similar to those of *O. sybotides*. He found that the spider preferentially attached linear stabilimenta to short radii ending near anchor threads. Physically, a spider on a horizontal orb web has most of its weight on the shortest radii ending near the anchor threads. When a spider adds linear stabilimenta, its position is aligned or partially aligned with the stabilimenta. Eberhard (1973) argued that this could be explained if the stabilimenta function as protection against visually orientated predators. From the perspective of tension regulation, however, another explanation is possible. Spiders are heavier when food satiated than when hungry. The increased weight of the spider would raise the thread tension of the web, so to shift their target to larger prey the spiders would need to decrease the tension of the radial threads. It may be possible to bias the weight load on the shortest radii ending near the anchor threads. The linear stabilimenta may serve to strengthen the short radial threads which bear the spider's weight disproportionally.

Prey-capture success is dependent on web structure, which is related to the prey interception rate and prey-catching behaviour of spiders (Chacón & Eberhard 1980). This study suggests that spiders tune their webs differently together with other engineering features (e.g. mesh size). The tension of the radial threads seems to be regulated at the hub and a higher tension on the radial threads serves to make the spider more sensitive towards smaller prey when hungry. The spiders seem to adjust their prey selection in response to their energetic state, regulating both web structure and prey-catching behaviour by modifying their web design.

I am extremely grateful to M. Yoshida, T. Miyashita and T. Masumoto for encouraging me during the early stage of my work. I also thank S. Yabuta, K. Nakata, S. Ishida and other members of the Laboratory of Animal Ecology, Kyoto University for helpful comments on the manuscript.

REFERENCES

Chacón, P. & Eberhard, W. G. 1980 Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bull. Br. Arachnol. Soc.* **5**, 29–38.

Charnov, E. L. 1976 Optimal foraging: attack strategy of a mantid. *Am. Nat.* **110**, 141–151.

Dusenbery, D. B. 1992 *Sensory ecology: how organisms acquire and respond to information*. New York: W. H. Freeman & Co.

Eberhard, W. G. 1972 The web of *Uloborus diversus* (Araneae: Uloboridae). *J. Zool. Lond.* **166**, 417–465.

Eberhard, W. G. 1973 Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J. Zool. Lond.* **171**, 367–384.

Herberstein, M. E., Abernethy, K. E., Backhouse, K., Bradford, H., De Crespigny, F. E., R., L. P. & Elgar, M. A. 1998 The effect of feeding history on prey capture behaviour in the orb-web spider *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Ethology* **104**, 565–571.

Klärner, D. & Barth, F. G. 1982 Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata, Nephila clavipes*; Araneidae). *J. Comp. Physiol.* A **148**, 445–455.

Landolfa, M. A. & Barth, F. G. 1996 Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *J. Comp. Physiol.* **179**, 493–508.

Masters, W. M. 1984*a* Vibration in the orbwebs of *Nuctenea sclopetaria* (Araneidae). I. Transmission through the web. *Behav. Ecol. Sociobiol.* **15**, 207–215.

Masters, W. M. 1984*b* Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). II. Prey and wind signals and the spider's response threshold. *Behav. Ecol. Sociobiol.* **15**, 217–223.

Murakami, Y. 1983 Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). *Oecologia* **57**, 72–77.

Riechert, S. E. & Luczak, J. 1984 Spider foraging: behavioral responses to prey. In *Spider communication: mechanisms and ecological significance* (ed. P. N. Witt & J. S. Rovner), pp. 353–385. Princeton University Press.

Robinson, M. H. & Robinson, B. 1970 The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. *Can. Entomol.* **102**, 641–655.

Sandoval, C. P. 1994 Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Funct. Ecol.* **8**, 701–707.

Uetz, G. W. & Hartsock, S. P. 1987 Prey selection in an orb-weaving spider: *Micrathena gracilis* (Araneae: Araneidae). *Psyche* **94**, 103–116.

Uetz, G. W., Johnson, A. D. & Schemske, D. W. 1978 Web placement, web structure, and prey capture in orb-weaving spiders. *Bull. Br. Arachnol. Soc.* **4**, 141–148.

Watanabe, T. 1999*a* Prey-attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. *Behav. Ecol.* **10**, 607–611.

Watanabe, T. 1999*b* The influence of energetic state on the form of stabilimentum built by *Octonoba sybotides* (Araneae: Uloboridae). *Ethology* **105**, 719–725.

Wirth, E. & Barth, F. G. 1992 Forces in the spider orb web. *J. Comp. Physiol.* A **171**, 359–371.