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DOES THE PRESENCE OF POTENTIAL PREY AFFECT WEB DESIGN IN *ARGIOPE KEYSERLINGI* (ARANEAE, ARANEIDAE)?

Marie E. Herberstein, **Anne C. Gaskett**, **Deborah Glencross**, **Simon Hart**, **Sue Jaensch** and **Mark A. Elgar:** Department of Zoology, University of Melbourne, 3010, Victoria, Australia

ABSTRACT. Orb-web spiders may anticipate their future prey environment by detecting the presence of prey and adjusting their web building behavior accordingly. Here we investigate the effect of different prey sizes and density on the web size and mesh height of the orb webs constructed by *Argiope keyserlingi*. The experimental design allowed the transmission of prey vibrations but prevented any capture. We found that *A. keyserlingi* constructed webs more frequently in the presence of prey, but did not alter the web size or mesh height of their webs.

Keywords: Orb web, mesh height, foraging, behavior

Orb-web spiders (Araneae, Araneidae) employ remarkable flexibility in their foraging behavior. For example, following periods of starvation, orb-web spiders increase the size of their webs and attack prey less selectively while sated spiders reduce web size and reject less profitable prey (e.g., Sherman 1994; Herberstein et al. 1998; Herberstein et al. 2000). Web construction is energetically the most expensive component of a spider's foraging effort (Opell 1998), and webs cannot be modified following completion. Decisions made during web construction influence subsequent capture success until a new web is built. Thus, it may be advantageous to design a web in anticipation of the future prey environment, rather than simply relying on past events.

Web-building spiders may make some preemptive foraging decisions in response to the density or size of potential prey. Sandoval (1994) concluded that the orb-web spider, *Parawixia bistriata* is able to exploit swarms of unusually large termite prey. *Parawixia bistriata* typically constructed small, finely meshed webs at night that trapped tiny dipteran prey (Sandoval 1994). At the onset of the rainy season, the spiders dramatically changed their activity patterns and web design. At this time, they built additional webs during the day with increased web area and mesh height (the average distance between capture spirals). Interestingly, the spiders seemed to anticipate the timing of the swarms: they changed their web design before the termites emerged, potentially using rainfall and humidity as cues (Sandoval 1994). Experimental evidence also suggests that spiders vary mesh height due to the presence of differently sized prey (Schneider & Vollrath 1998). In a similar case, *Zygiella x-notata* (Pasquet et al. 1994) anticipated prey density before web construction. More abundant potential prey induced the construction of smaller webs earlier in the evening. Presumably, smaller webs were finished more quickly, allowing prey capture to commence earlier.

Here, we examine the effect of the size and number of potential prey on the web building behavior of *Argiope keyserlingi* Karsch 1878. We predict that larger potential prey will induce increased mesh height, and that higher prey density will decrease web area.

Experiments were conducted in March and April 1998 and January 1999, using adult *Argiope keyserlingi* collected in Sydney and Brisbane, Australia. In the laboratory, spiders were housed in upturned plastic cups (13.5 × 9 × 9 cm) where they were watered and fed blow flies (*Lucilia cuprina*, Diptera) ad libitum. The spiders were unable to construct a functional web in the upturned cups apart from a few supporting threads. Thus, prey capture did not involve a web. Instead, the spiders generally grasped the flies buzzing around in the cup.

The spiders were starved for four days prior to experimentation. This ensured that the spiders' energetic status was uniform. Additionally, by depriving spiders of web-building space we minimized the influence of previously built webs on the foraging decisions made during experimentation (see Herberstein et al. 2000). The spiders were weighed and transferred to three-dimensional frames (40 × 50 × 8.5 cm) and allowed to construct complete webs in the presence of different sizes and densities of potential prey. Frames either contained 30 *Drosophila* (Diptera), one blow fly, or 30 blow flies. Prey were held in identical plastic jars (diameter: 4.7 cm, height: 6.8 cm), covered by fine mesh. This setup allowed prey movement and the transmission of airborne vibrations created by the buzzing of the flies, but prevented capture.

We selected the two prey types because they differ in body length (blow flies: 7.8 ± 0.12 mm, $n = 20$; *Drosophila*: 2.5 ± 0.06 mm, $n = 20$). To control for differences in weight and therefore energy return, treatment one consisted of 30 *Drosophila* per jar. This approximated the weight of one blow fly per jar as used in treatment two (one blow fly: 0.022 ± 0.0006 g, $n = 39$; 30 *Drosophila*: 0.021 ± 0.0004 g, $n = 21$). The third treatment, 30 blow flies, allowed comparison of the webs built for different prey densities, and for different prey types. Only the first web spun by each individual was measured and used to evaluate the effects of the prey treatments. This minimized the influence of previous foraging history on web design. We estimated the web area and the mesh height using various formulae that only require a few measurements (Herberstein & Tso 2000).

Statistical analyses were conducted using Systat 5.2 (Wilkinson 1992) and G●Power (Buchner et al. 1997). Data were log transformed if they were not normally distributed (Kolmogorov-Smirnov). Web area, mesh and spider weight were compared using ANOVA with treatment and year as factors. All values are mean ± SE unless stated otherwise.

Data from 49 spiders were included in the analyses. There was no significant difference in body weight between the spiders used in 1998 and 1999 (for 1998/1999: 30 blow flies 0.255 ± 0.028 g / 0.266 ± 0.023 g, one blow fly 0.269 ± 0.020 g / 0.293 ± 0.029 g, 30 *Drosophila* 0.253 ± 0.019 g / 0.219 ± 0.038 g; $F_{1,43} = 0.00001$, $P > 0.05$). The weight of spiders allocated to the three treatments was similar ($F_{2,43} = 1.37$, $P > 0.05$), and there was no interaction effect of year and treatment ($F_{2,43} = 0.61$, $P > 0.05$). Web area (Fig. 1) did differ between the two years ($F_{1,43} = 30.79$, $P < 0.01$): in 1999 spiders constructed larger webs compared to the previous year. This is probably because spiders were maintained in the laboratory for approximately two months before use in 1998, whereas the experiment was commenced within two weeks of collection in 1999. Varying the size and density of potential prey did not affect web size ($F_{2,43} = 0.007$, $P > 0.05$), nor was there an interaction effect between year and treatment ($F_{2,43} = 0.79$, $P > 0.05$). The size of the frame, and thus the available web building space may have limited the foraging decision of the spiders. However, the maximum web size observed (approx. 850 cm^2) was less than half of that available (2000 cm^2).

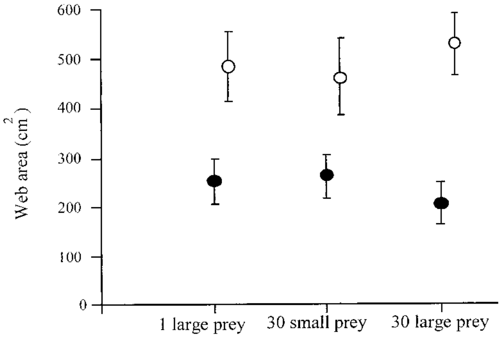

Figure 1.—The mean (± SE) area of webs constructed in the presence of one large prey, 30 small prey and 30 large prey in 1998 (●) and 1999 (○).

Mesh height (Fig. 2) was similar in both years ($F_{1,43} = 1.40$, $P > 0.05$) and was unaffected by prey treatment ($F_{2,43} = 0.34$, $P > 0.05$). Contrary to prediction, the presence of large prey did not result in larger mesh height compared to small prey. Power analysis revealed that our sample size was sufficient to detect a treatment effect ($1 - \beta = 0.68$). Again, the interaction between year and treatment was not significant ($F_{2,43} = 1.63$, $P > 0.05$).

These results are contrary to both of our predictions, and the results of previous studies (Schneider & Vollrath 1998; Pasquet et al. 1994) that found a relationship between the size and density of prey and web design. However, these previous experiments released prey into the web-building frames with the spiders. In the laboratory, we frequently ob-

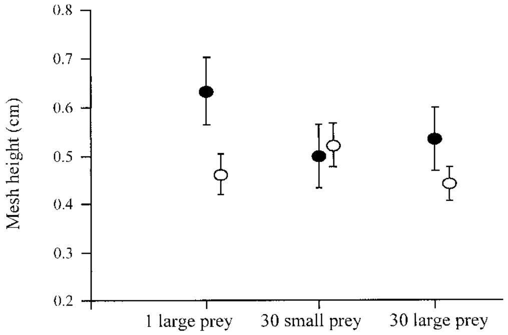

Figure 2.—The mean (± SE) mesh height for webs constructed in the presence of one large prey, 30 small prey and 30 large prey in 1998 (●) and 1999 (○).

Table 1.—The mean (±SE) for the web area and mesh height of spiders constructing webs when there are no flies, one fly or 30 flies enclosed with the spider.

Treatment	Sample size	Web area (cm^2)	Mesh height (cm)
No flies	11	1053.0 ± 112.6	0.517 ± 0.02
1 fly	12	1015.3 ± 108.4	0.503 ± 0.04
30 flies	14	1086.8 ± 100.3	0.517 ± 0.02

serve orb-web spiders housed in both frames and cups grasping and consuming prey without webs. As the spiders in these previous experiments (e.g., Schneider & Vollrath 1998) had the opportunity to capture prey during web building, it is unclear whether their webs represented an anticipatory prey assessment, or past experience. In the present study, enclosing the prey in mesh-covered jars prevented such confounding effects. However, the absence of any significant difference in web design between the prey treatments suggests two explanations; either our experimental design did not allow the spiders to detect the prey, or *A. keyserlingi* does not make preemptive adjustments to web mesh size and area to suit varying sizes and numbers of potential prey.

To distinguish between these two explanations, we repeated the experiments in January and May 2000 using identical methods but including a control treatment (no flies), where we measured web area and mesh height in a sub-sample and the frequency of web construction in a larger sample of individuals. We predicted that, if these spiders can detect airborne vibrations created by the enclosed flies, we should find differences between treatments that included no blow flies (empty container), one blow fly and 30 blow flies. Any difference in the web-building behavior between the no-fly treatment *versus* the fly treatments would indicate that the spiders were able to detect the presence or absence of prey in the containers.

We found no significant differences in mesh size ($F_{2,\,34} = 1.28$, $P > 0.05$) or web area ($F_{2,\,34} = 0.29$, $P > 0.05$; Table 1) between the treatments. However, fewer spiders constructed a web when no flies were present (16 out of 24 spiders). In contrast, almost all spiders (21 out of 22) presented with a jar of 30 blow flies, and 19 of 26 spiders presented with only one blow fly, built a web. We compared these frequencies using a contingency table, which revealed that the likelihood to build a web was significantly different between the three treatments ($\chi^2 = 6.3$, $P = 0.044$). These results indicate that our experimental design allowed the spiders to detect the presence of potential prey, and they adjusted the frequency of web construction accordingly (see also Pasquet et al. 1994), but not web size or design. It may be that spiders are unable to detect differences between the airborne vibrations created by different sizes and densities of prey. Alternatively, spiders may be able distinguish between prey densities and sizes, but do not alter the web design in response. Behavioral tests, such as those presented here, cannot distinguish between these two alternatives.

Adjusting web building frequency in response to the presence of prey may reflect risk sensitivity, where foragers react to variation in prey encounter rates by changing web sites or web size (e.g., Herberstein et al. 2000; Gillespie & Caraco 1987). Web building spiders invest a substantial amount of energy into silk production and web construction (e.g., Peakal & Witt 1976; Higgins & Buskirk 1992), and rely on prey coming into contact with the web. As such, prey encounter can be highly unpredictable and spiders may conserve energy by not building a web when there is little indication of abundant prey. In contrast, when prey is in close proximity and in high density, increased web building activity may allow these spiders to exploit abundant prey.

Numerous field studies have also failed to find a consistent relationship between mesh height and prey size (McReynolds & Polis 1987; Herberstein & Elgar 1994; Herberstein & Heiling 1998). Simulations (Eberhard 1986) and laboratory manipulations (Nentwig 1983) further confirm that orb-webs do not function as ''sieves.'' Mesh height may fulfill alternative functions. A narrow mesh may facilitate the retention of larger prey, as more threads are in contact with the item (Eberhard 1990). However, more spiral turns also reflect more light thus increasing the visibility of the web to prey (Craig 1986; Craig & Freeman 1991). Mesh height may therefore indicate a compromise between prey retention and web visibility. A larger capture area results in a higher prey interception rate (Chacón & Eberhard 1980) and by increasing the distance between sticky spirals spiders may enlarge overall capture area without greater energy expenditure. Accordingly, food deprived spiders commonly increase web area to enhance prey encounter (Sherman 1994; Herberstein et al. 2000). Finally, it seems unlikely that spiders would tailor their webs for small and possibly unprofitable prey. Spiders often ignore small prey entangled in the web (Uetz & Hartsock 1986; Herberstein et al. 1998) which may subsequently escape. Logically, any web should target profitable prey items worthy of attack and more permanent retention through silk wrapping.

Web design reflects several trade-offs between the different functions of various web elements and is influenced by internal physiological states and previous experience. Interpreting orb-webs as size filters is likely to oversimplify this complex foraging investment.

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LITERATURE CITED

Buchner, A., F. Faul & E. Erdfelder. 1997. G●Power: a priori, post-hoc, andcompromise power analyses for the Macintosh (Version 2.1.2; Computer program). University of Trier: Germany.

Chacón, P. & W.G Eberhard. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs with considerations of how orb webs trap prey. Bulletin of the British Arachnological Society 5:29–38.

Craig, C.L. 1986. Orb-web visibility: The influence of insect flight behaviour and visual physiology on the evolution of web designs within the Araneoidea. Animal Behaviour 34:54–68.

Craig, C.L. & C.R. Freeman. 1991. Effects of predator visibility on prey encounter: A case study on aerial web weaving spiders. Behavioral Ecology & Sociobiology 29:249–254.

Eberhard, W.G. 1986. Effects of orb-web geometry on prey interception and retention. Pp. 70–100, *In* Spiders—Webs, Behavior, and Evolution. (W.A. Shear, ed.). Stanford Univ. Press. Stanford, California.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Annual Review of Ecological Systems 21:341–372.

Gillespie, R.G. & T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. Ecology 68:887–899.

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

Herberstein, M.E., C.L. Craig & M.A. Elgar. 2000. Foraging strategies and feeding regimes: Web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). Evolutionary Ecology Research 2:69–80.

Herberstein, M.E. & M.A. Elgar. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneoidea): Nocturnal and diurnal orb-weaving spiders. Australian Journal of Ecology 19:451–457.

Herberstein, M.E. & A.M. Heiling. 1998. Does mesh height influence prey length in orb-web spiders? European Journal of Entomology 95: 367–371.

Herberstein, M.E. & I.M. Tso. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea: Araneae). Journal of Arachnology 28(2):180–184.

Higgins, L.E. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Animal Behaviour 44:485–499.

McReynolds, C.N. & G.A. Polis. 1987. Ecomorphological factors influencing prey use by two sympatric species of orb-web spiders, *Argiope* *aurantia* and *Argiope trifasciata* (Araneidae). Journal of Arachnology 15:371–383.

Nentwig, W. 1983. The non-filter function of orb webs in spiders. Oecologia 58:418–420.

Opell, B.D. 1998. Economics of spider orb-webs: The benefits of producing adhesive capture thread and of recycling silk. Functional Ecology 12:613–624.

Pasquet, A., A. Ridwan & R. Leborgne. 1994. Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. Animal Behaviour 47:477–480.

Peakal, D.B. & P.N. Witt. 1976. The energy budget of an orb web-building spider. Comparative Biochemistry & Physiology A 54:187–190.

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

Schneider, J.M. & F. Vollrath. 1998. The effect of prey type on the geometry of the capture web of *Araneus diadematus*. Naturwissenschaften 85: 391–394.

Sherman, P. 1994. The orb web: An energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. Animal Behaviour 48:19–34.

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

Wilkinson, L. 1992. 'Systat: Statistics.' Version 5.2, Systat: Evanston.

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