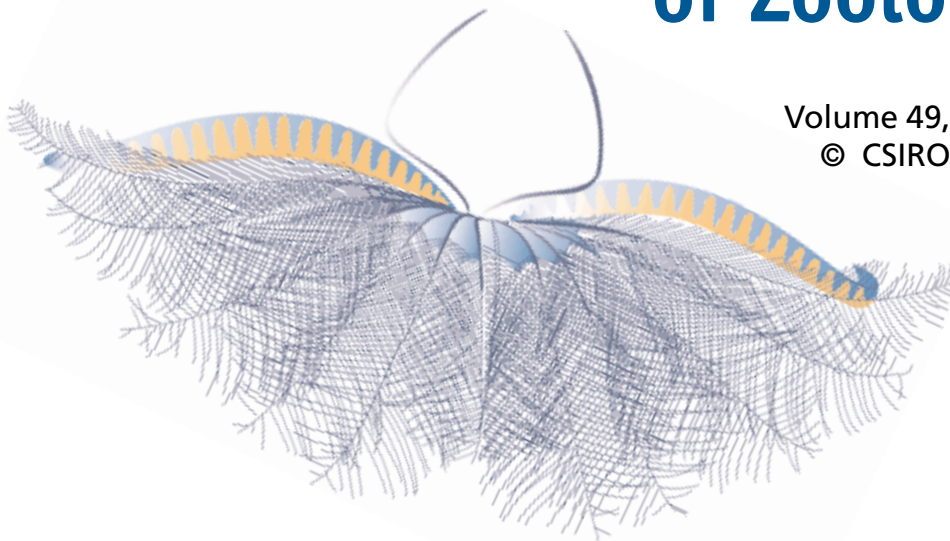


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The effect of predator–prey distance and prey profitability on the attack behaviour of the orb-web spider *Argiope keyserlingi* (Araneidae)

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Abstract

The foraging behaviour of central-place foragers is thought to be strongly influenced by the distance between the forager and the food source (predator–prey distance). Orb-web spiders are uniquely suited for investigating this idea because they make active foraging decisions towards prey entangled in the web, and they define the dimensions of their foraging arena when they construct the web. Here we manipulate the physiological condition of *Argiope keyserlingi* and present the spiders with prey of varying quality, in terms of size and accessibility (location within the web and distance from the spider). We found that these spiders adjust their foraging behaviour primarily in response to their physiological condition but, in contrast to other central-place foragers, are indiscriminant of predator–prey distance or the likelihood of escape of the prey. We suggest that these factors are incorporated into the design of the web, and thus increase foraging success through efficient web design.

Introduction

It is well established that animals adjust their foraging behaviour according to the energetic value or profitability of prey, which may depend on the size and palatability of the prey, its physical threat, its probability of escape, and the physiological state of the forager (e.g. Stephens and Krebs 1986). Less attention has focussed on the relevance of the location of prey relative to the predator, which may be an important factor because the energy expended in pursuing and capturing prey is a crucial cost (Bell 1991; Shafir and Roughgarden 1998). For example, the greater the predator–prey distance, the lower the net energetic profit for the predator (Schoener 1971) and the greater the cost to the predator with respect to escape of the prey or exposure (Shafir and Roughgarden 1998). Therefore, prey items should only be pursued to the outermost limit for efficient foraging, and ignored beyond that point (Schoener 1971). Studies of this form of central-place foraging show that the probability of attacks by the predator decreases with increasing distance from prey in mantids (Charnov 1976) and lizards (Shafir and Roughgarden 1998).

The behaviour of web-building spiders suggests a novel dimension to studies of the dynamics of central-place foraging because the limits of their foraging arena are immediately evident: an orb-web spider cannot forage beyond the web and it cannot adjust this boundary after the web has been constructed. In addition, orb-web spiders invest a substantial and measurable amount of energy in constructing their foraging arena. Web construction is the most energetic aspect of foraging for web-building spiders (Peakall and Witt 1976; Craig 1989; Sherman 1994), a cost that must be balanced against the expected reward (Sherman 1994; Herberstein *et al.* 2000).

Spiders can vary the dimensions of the web and thus the size of their effective foraging arena (e.g. Higgins and Buskirk 1992; Sherman 1994; Lubin and Henschel 1996; Herberstein *et al.* 2000). For example, incorporating less silk may save energy but results

in a smaller capture area, thus decreasing the chance of encountering prey. Conversely, webs cannot be extended indefinitely because, apart from structural limitations, the cost of constructing such a web would vastly outweigh the energetic gain through increased prey capture (Eberhard 1986).

Despite a comprehensive understanding of the dynamics of web construction, relatively little is known about the behaviour of spiders within their foraging arena once webs are constructed. There are documented accounts of orb-web spiders ignoring or removing unpalatable or dangerous prey from their webs (Riechert 1991; Herberstein *et al.* 1998), but it is not clear whether central-place foraging predictions are also applicable to spiders foraging within their web.

With this in mind, we investigated whether spiders evaluate predator–prey distance and adjust their attack behaviour accordingly. Specifically, we anticipate that spiders are less likely to attack prey entangled at a greater distance. This may be because the prey have a greater chance to escape before the spider arrives. Similarly, travel to prey may be impeded in the upper half of the vertical web, as the spider has to combat gravitational forces (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994). Furthermore, relative costs and benefits of pursuing and capturing prey will ultimately vary with the energy reserves of the spiders: satiated individuals may reject prey that food-deprived spiders would attack (Herberstein *et al.* 1998). Finally, as spiders construct their foraging arena, it is essential to monitor any variation within the web. Thus, different web regions may retain prey for different lengths of time, affecting the relative chance of escape and, consequently, the behaviour of the spider. We addressed these questions using the St Andrew's Cross Spider, *Argiope keyserlingi* Karsch, a large orb-web spider common in a variety of habitats along the eastern seaboard of Australia.

Methods

Experiments were conducted from April to July 1998. Juvenile females of *A. keyserlingi* were collected from several sites in suburban Sydney and were raised in the laboratory in upturned plastic cups (13.5 cm × 9 cm). Upon reaching maturity they were randomly allocated to either a food-deprived or food-satiated feeding regime. Food-deprived spiders received one fly (*Lucilia cuprina*: Diptera) every four days, and food-satiated spiders received two flies per day for approximately two weeks. The spiders were hand-fed during the experiments to ensure that all prey items were ingested. Consequently, food-deprived spiders weighed significantly less than food-satiated spiders at the completion of the feeding regime in each experiment (Table 1). At the end of the feeding regimes spiders were transferred to three-dimensional perspex frames (50.5 cm × 40.0 cm × 9.0 cm) where they constructed functional orb-webs. Web spinning was encouraged by the inclusion of a small, mesh-covered plastic cup containing approximately five flies (see Pasquet *et al.* 1994). Different individuals were used for each experiment.

Foraging decisions and the distance between predator and prey

Single fruit flies (*Drosophila* sp.: Diptera) were inserted into the newly constructed webs of food-deprived ($n = 12$) and food-satiated spiders ($n = 18$) at distances of 5 and 10 cm from the spider at the junction of a radial and a spiral thread. Each trial was separated by at least 15 min to allow the spider to return to the central hub after the trial. The order of distances was randomised. Prey items that did not struggle

Table 1. Mean (\pm s.e.) weight (g) of food-deprived and food-satiated spiders in each experiment

Experiment	Food-deprived spiders	Food-satiated spiders	Statistics
Prey retention	0.188 \pm 0.008	0.334 \pm 0.013	$t_{36} = -10.1$, $P = 0.0001$
Prey distance	0.252 \pm 0.010	0.399 \pm 0.019	$t_{28} = -2.324$, $P = 0.015$
Prey location	0.232 \pm 0.011	0.383 \pm 0.015	$t_{45} = 2.314$, $P = 0.015$

continuously were removed from the web and replaced with new prey after 15 min had elapsed. Spiders located prey by tugging the radial threads and then moving rapidly towards the prey, which were grasped in the chelicerae and/or wrapped upon contact. The attack behaviour was recorded using a video camera with a stopwatch. The timing procedure followed Masters and Moffat (1983). The 'attack' time of the spiders was determined by video analysis, and was defined as the time between the initial rapid movement towards the prey and making contact with the prey item. In general, once spiders started to approach the prey, they rarely abandoned the attack. Prey items were removed after capture in order to maintain the satiation level of the spider.

Foraging decisions and the location of the prey in the orb-web

Food-deprived ($n = 12$) and food-satiated ($n = 26$) spiders were subjected to feeding trials that were recorded by a video camera. A single prey item was introduced into the web 10 cm directly above or below the hub at the junction of a radial and a spiral thread. Two different prey types – crickets (*Achaeta domestica*) and *Drosophila* – were tested in separate trials that were at least 15 min apart. Location and prey types were randomly ordered. Prey items that did not struggle continuously were removed and replaced after 15 min had elapsed. Prey items were removed after capture in order to maintain satiation level. The attack times were determined by video analysis.

Retention of prey and location of impact

The capture area of the webs of food-deprived ($n = 23$) and food-satiated ($n = 15$) spiders was divided into four different regions: the inner and outer region of the upper and lower web hemisphere, and named A, B, C and D (Fig. 1). These regions were separated by the mid-point of the vertical radii (not including the hub) of the upper (r_u) and lower hemisphere (r_l). The number of capture spirals within each region was counted to determine the mesh height for each region (see Herberstein and Tso 2000). The spiders were removed from the web and, with soft forceps, a struggling fly was introduced into each of the four regions at the

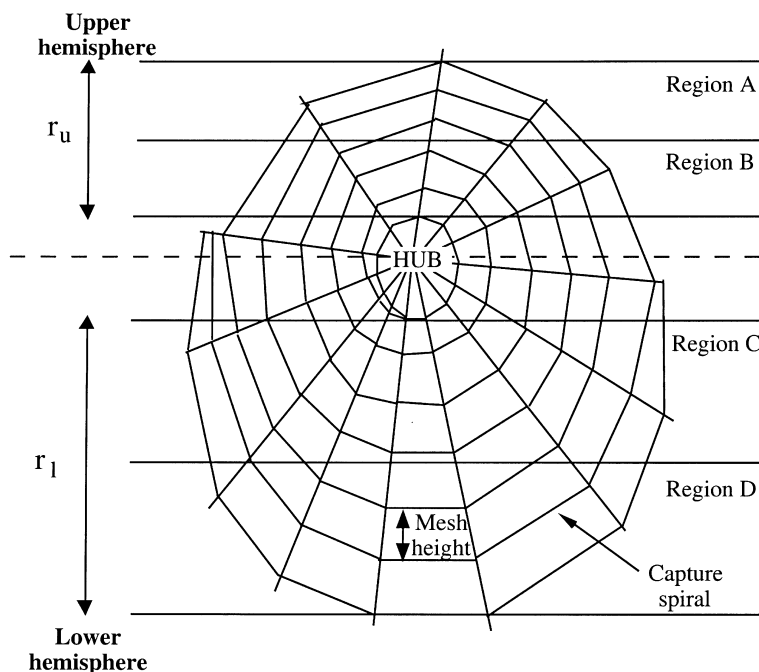


Fig. 1. Schematic representation of an orb web, illustrating the four regions (Region A: outer region of upper hemisphere; Region B: inner region of upper hemisphere; Region C: inner region of lower hemisphere; Region D: outer region of lower hemisphere) within the web.

Table 2. Log-linear modeling for attack frequencies of *A. keyserlingi* in response to feeding regime (deprived/satiated) and spider–prey distance (5/10 cm)

Modification of the initial log-linear model by removing non-significant interactions in order of highest complexity resulted in a model that explained the data (likelihood ratio = 0.7913, d.f. = 3, $P = 0.852$)

Test	d.f.	Likelihood ratio	<i>P</i>
Main effects:			
Feeding regime	1	0.02	0.88
Distance	1	0.35	0.55
Attacks	1	0.82	0.36
Interactions:			
Distance by attacks	1	0.00	0.97
Feeding regime by attacks	1	32.24	0.00
Feeding regime by distance by attacks	1	0.35	0.55

junction of a radial and a spiral thread. A stopwatch was used to record the time taken until the fly escaped from each region. Escape times that were greater than 5 min were treated as a 'capture', because these spiders generally capture prey within 60 s. Retention times of flies that did not struggle consistently were not included in the analysis.

All statistical analyses were performed using SYSTAT 5.2 (Wilkinson 1992). Data were tested for normality prior to analysis with parametric tests. ANOVAs were applied to the mesh and prey-retention data. Log-linear modeling assessed the impact of multiple factors on the foraging decisions of the spiders; non-significant interactions were removed in order of highest to lowest complexity to achieve the simplest model. Repeated-measures ANOVAs were used to analyse attack time of individual spiders towards different prey in different web locations.

Results

Foraging decisions and the distance between predator and prey

The physiological condition of *A. keyserlingi* was the dominant influence on foraging decisions. Food-deprived spiders attacked fruit flies significantly more frequently than food-satiated spiders (Table 2; Fig. 2). However, prey were attacked or rejected irrespective of predator–prey distance (Table 2). In addition, *A. keyserlingi* were able to capture prey in similar times, regardless of the distance that prey were located from the hub. There was no discernable difference in the time taken to capture prey at the two distances from the hub by either food-deprived (independent *t*-test: $t_{16} = 0.500$, $P = 0.624$) or food-satiated (independent *t*-test: $t_8 = 0.407$, $P = 0.695$) spiders.

Foraging decisions and the location of the prey in the orb-web

Location of the prey in the upper or lower web hemisphere had little effect on the foraging decisions of *A. keyserlingi*. Rather, the physiological condition of the spiders determined whether they attacked or rejected prey (Table 3). Accordingly, food-deprived spiders showed less selectivity in prey type (Fig. 3), attacking *Drosophila* and crickets more frequently than did food-satiated spiders. In addition, there were no significant differences between the attack times of each spider towards different types of prey at different locations (crickets: $F_{1,15} = 0.0003$, $P = 0.987$; *Drosophila*: $F_{1,4} = 1.74$, $P = 0.258$).

Retention of prey and location of impact

Although food-deprived spiders spun larger webs than did food-satiated spiders (ANOVA: $F_{1,17} = 15.827$, $P < 0.001$) there was no difference in mesh height (ANOVA: $F_{1,35} = 1.497$,

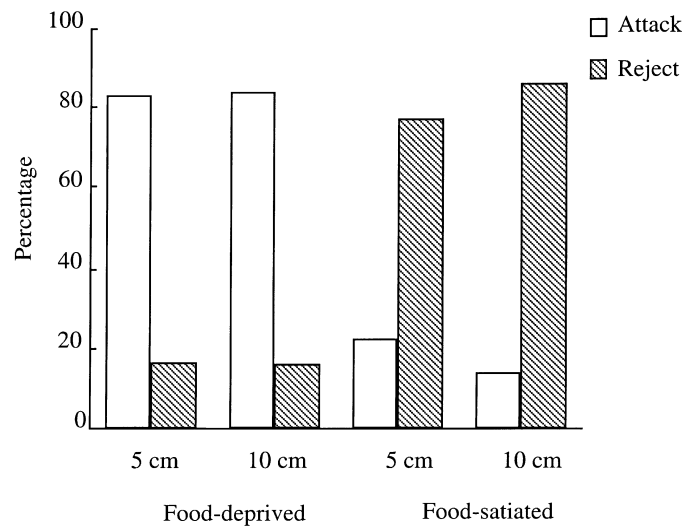


Fig. 2. The percentage of attacks by food-deprived and food-satiated *A. keyserlingi* on *Drosophila* at 5 cm and 10 cm from the spider ($n = 71$).

$P = 0.229$). Thus, data from both treatments were combined to compare within-web variation. We found significant differences in the mesh height of different regions within the orb-web (ANOVA: $F_{3,105} = 12.087$, $P < 0.001$; Fig. 4a). The finest mesh was spun in the outer region of the lower web hemisphere. This corresponded to the region in which it took prey longest to escape (ANOVA: $F_{3,96} = 2.820$, $P = 0.043$; Fig. 4b). There was no difference in the retention times of webs constructed by food-deprived or food-satiated spiders (ANOVA: $F_{1,32} = 2.518$, $P = 0.122$).

Table 3. Log-linear modeling for attack frequencies of *A. keyserlingi* in response to feeding regime (deprived/satiated), prey type (*Drosophila*/cricket) and prey location (above/below hub)

Modification of the initial log-linear model by removing non-significant interactions in order of highest complexity resulted in a model that explained the data (likelihood ratio = 2.9443, d.f. = 8, $P = 0.938$)

Test	d.f.	Likelihood ratio	P
Main effects:			
Feeding regime	1	0.51	0.47
Prey type	1	0.77	0.38
Location	1	0.54	0.46
Attacks	1	0.04	0.83
Interactions:			
Feeding regime by attacks	1	17.80	0.00
Prey type by attacks	1	6.59	0.01
Location by attacks	1	0.31	0.57
Feeding regime by prey type by attacks	1	5.51	0.01
Feeding regime by location by attacks	1	0.03	0.86
Prey type by location by attacks	1	0.05	0.83
Feeding regime by prey type by location by attacks	1	1.30	0.25

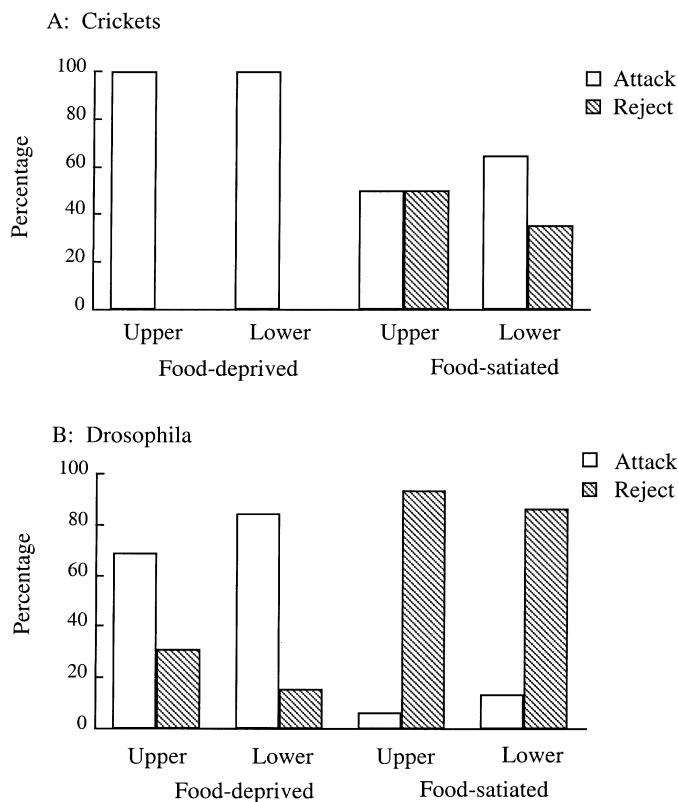


Fig. 3. The percentage of attacks by food-deprived and food-satiated *A. keyserlingi* on (A) crickets ($n = 61$) and (B) *Drosophila* ($n = 72$), in the upper and lower hemispheres of the web.

Discussion

In contrast to our prediction, and the behaviour of many central-place foragers, the active foraging decisions of *A. keyserlingi* do not appear to be influenced by predator–prey distance. The only discernible factor that affects the behaviour of these spiders after web construction is their physiological condition: satiated spiders were less likely to pursue unprofitable prey (see also Herberstein *et al.* 1998). Thus, the net energetic return from small prey may be less for food-satiated spiders than for food-deprived spiders.

The profitability of a prey item in the encounter-at-a-distance model depends, in part, on the distance of the prey from the predator (Charnov 1976; Shafir and Roughgarden 1998). Thus, prey items close to a predator may be more profitable than identical items further away. In addition, the distance at which a sit-and-wait predator is prepared to attack should decrease as success at capturing prey increases (Shafir and Roughgarden 1998). There are at least two explanations why *A. keyserlingi* did not behave according to these predictions. First, spiders may be unable to discriminate between the value of prey at different distances. However, the spiders were able to discriminate between different sizes and thus values of prey (see also Herberstein *et al.* 1998). Second, the profitability of prey in terms of pursuit costs and chance of escape may not vary throughout the web, resulting in no probability gradient within the foraging arena. In other words, no matter where prey

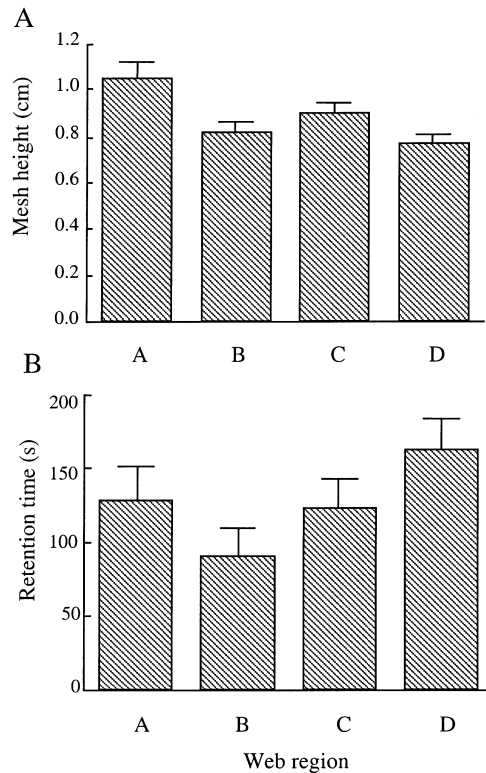


Fig. 4. (A) The mean (\pm s.e.) mesh height of each of the four web regions (A–D). (B) The mean (\pm s.e.) prey-retention time of prey entangled in each of the four web regions (A–D).

are entangled, the spider is equally likely to execute a successful capture. Our observations on pursuit times support this idea: *A. keyserlingi* captured prey in similar times irrespective of their distance or location relative to the spider.

Do spiders manipulate their foraging arena in order to counteract the effect of predator–prey distance that influences the foraging decisions of many other sit-and-wait foragers? In order to create uniform capture probabilities, orb-web spiders must modify the web at locations at which there is a high risk of prey escaping. For example, vertical web asymmetry, where the upper hemisphere of the web is smaller than the lower hemisphere, is common in araneoid spiders (Heiling and Herberstein 1998; Japyjassu and Ades 1998; Herberstein and Heiling 1999). It has been suggested that this web design minimises the time it takes the spider to attack prey even in the ‘high risk’ upper hemisphere, because spiders may take longer to move against, rather than with, gravity (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994). However, our data do not support this idea: there was no difference in the time that spiders took to reach prey in either the upper or lower hemisphere of the web.

Orb-web spiders may also influence the probability of successful prey capture by adjusting the height of the web mesh. We found significant within-web variation in mesh height of both food-satiated and food-deprived animals. Specifically, mesh height

decreased in the lower web hemisphere towards the periphery. We found that prey took longest to escape from this 'high risk' area, which was furthest from the hub (but see Nentwig 1983; Heiling and Herberstein 1998). Effectively, this means that any prey intercepted in this area will contact more of the sticky spirals and these may delay their escape efforts until the spider arrives (Eberhard 1986).

The second advantage of building a finer mesh in the periphery of the lower hemisphere may be an increase in capture of larger prey (Olive 1980). After impact, prey tumble down the web as a result of gravity and the outer region of the lower hemisphere provides the last opportunity to ensnare the prey. A narrow mesh, together with an increase in the size of the lower web hemisphere, may arrest prey that would otherwise continue to tumble off the web. This is especially crucial for large prey because their greater weight may require more capture spirals to halt their momentum (Olive 1980, 1981; Nentwig 1982; Eberhard 1986). The value of this design is most evident and well documented for the ladder webs build by araneids such as *Tylorida* sp. (Robinson and Robinson 1972; Eberhard 1980; Forster and Forster 1985). By vertically elongating their webs, these spiders increase the chance that enough of the sticky spirals will adhere to the slippery bodies of moth prey, and thereby halt the momentum and motion of the sliding prey (Stowe 1986).

It seems that the limiting factor of predator–prey distance for central place foragers has been overcome in at least one species. Because *A. keyserlingi* does not extend the boundaries of its web indefinitely, the size and design of the web may reflect an assessment of the appropriate predator–prey distance at which foraging is efficient and an adequate energy intake is ensured. Prey within this arena should, in general, always be attacked except in cases where prey poses a threat to the spider (see Herberstein *et al.* 1998).

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