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Memory of captured prey in three web spiders (Araneae: Araneidae, Linyphiidae, Tetragnathidae)

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Abstract We gave three web spiders, *Argiope argentata* (Araneidae), *Nephila clavipes* (Tetragnathidae) and *Neriene peltata* (Linyphiidae), large and small prey which we then removed from the spiders' webs. Following prey removal the spiders searched by walking around the web and pulling on its threads for several minutes, stopping when allowed to find the prey. Spiders that captured larger prey searched for longer. Searching behaviour was different from the spiders' responses to disturbance and did not appear to be elicited by proximal cues. Instead, the spiders formed memories of captured prey that included details about prey size and freshness.

Key words *Argiope* · *Nephila* · *Neriene* · Memory · Web spiders

Introduction

Some of the most remarkable studies of cognition in spiders have featured visually orienting hunters. A striking example is the jumping spider *Portia fimbriata*, a hunter of other spiders and insects that uses an extensive repertoire of programmed prey-specific and trial-and-error strategies (Jackson and Blest 1982; Jackson and Hallas 1986 a,1986 b; Jackson and Wilcox 1993 b,1998; Li and Jackson 1996). *P. fimbriata* attacks web spiders with web-borne vibratory signals (Jackson and Blest 1982), exploiting and sometimes causing distracting disturbances on the web of its prey (Wilcox et al. 1996; Jackson and Wilcox 1998). It mimics the male courtship signal of another species of jumping spider to lure females out of their nests (Jackson and Wilcox 1990, 1998; Jackson and Li 1997), and follows stalking routes that temporarily lead it away from the prey without having it in sight (Jackson and Wilcox 1993a, 1998; Tarsitano and Jackson 1994, 1997).

The uniquely developed visual nervous system of these spiders might be thought largely responsible for their cognitive abilities. Indeed, spiders that hunt by building webs are often seen as mindless automata that accomplish web-building by "instinct" alone (e.g. Gertsch 1979). But there are many indications that the cognitive abilities of web spiders that do not hunt visually are quite extensive. There are accounts that suggest memory of the spiders' own movements (Bartels and Baltzer 1928; Bartels 1929; Barth and Seyfarth 1971; Seyfarth and Barth 1972; Seyfarth et al. 1982; Görner and Claas 1985; Eberhard 1988; Ades 1989), of experience in aggressive contests (Whitehouse 1997), of experience in web building and prey capture and its effect on web building (Heiling and Herberstein 1999, and see Herberstein and Heiling 1999 for the effect of the spiders' increasing weight on web building; Venner et al. 2000), of stimuli associated with various kinds of prey (Bays 1962), and of the location of the spiders' retreat (LeGuelte 1969, 1970). The study of cognition in web spiders bears on the level of performance possible with a brain lacking exceptional development of the visual system, and on the general conditions under which cognition may evolve.

One indication of cognition in web spiders comes from their behaviour when they lose prey they have captured. Web spiders generally forage by spinning a snare (Foelix 1982) and waiting almost motionless for prey to be intercepted. But if their prey is taken by a natural enemy or an observer, some spiders engage in a very distinctive behaviour. They walk around the web and pluck or pull on its threads (Baltzer 1923; Vollrath 1979a; Rypstra 1981; Ades 1991). Similar behaviour was exhibited by female *Miagrammopes animotus* Chickering (Uloboridae) when their eggssacs were taken away (B. Opell, personal communication). This behaviour appears to be searching and is very likely to provide information to the spider about

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the web and its contents (Suter 1978; Klärner and Barth 1982; Landolfa and Barth 1996; Weissmann and Vollrath 1999). This evidence suggests that these spiders form memories of the prey they have captured, but this hypothesis has not yet been tested explicitly. If true, this ability could be very useful for web spiders to relocate previously stored prey that they may have lost due to partial web destruction or kleptoparasites.

In this paper we analyse the behaviour of three species of web spiders after we removed prey from their webs. We tested the hypotheses that the spiders' behaviour was searching (and not elicited by the disturbance of stealing the prey), that searching indicated memory of captured prey (not elicited by immediate cues remaining on the web), and that specific prey features were included in the spiders' memory.

Methods

Spider species

The spiders, *Argiope argentata* (Araneidae), *Nephila clavipes* (Tetragnathidae) and *Neriene peltata* (Linyphiidae), hereafter referred to by their generic names, were chosen because they were convenient to study, locally abundant and belonged to different families. Our choice was arbitrary with respect to their web architecture and behaviour, except that we did preliminary work to find species from which it was possible to steal prey with minimum disturbance. For example, it is not convenient to steal prey from a species that does not suspend prey from its web, such as the pholcid *Physocyclus globosus*, because when disturbed they retreat with the prey still in their mouthparts (R. L. Rodríguez S., unpublished work). The spiders' web and prey-capture behaviour are as follows. *Neriene* spins a typical linyphiid sheet web of non-sticky thread (Foelix 1982). In prey capture, *Neriene* first bites the prey and then wraps it in silk. Feeding does not occur at the capture site; instead, *Neriene* returns to the spot in the web where it had been before prey capture, behaving as though there were a hub on the web (R. L. Rodríguez S., unpublished work). Both *Argiope* and *Nephila* spin orbwebs with hubs (Foelix 1982). *Nephila* bites the prey before wrapping it in silk (unless it is very small), returns to the hub, rotates and produces several new dragline attachment points, suspends the prey from the hub, and feeds (Robinson and Mirick 1971; Gorb et al. 1998). *Argiope* wraps the prey in silk before biting it (except for lepidopteran or small prey), and feeds at the hub but does not suspend the prey there (Robinson 1969; Robinson and Robinson 1970).

Prey species

We used large and small prey in rough proportion to the spiders' size: *Drosophila* flies for *Neriene*, orthopterans (mostly tettigoniids) captured in the field for *Argiope*, and *Acheta domestica* crickets for *Nephila* (Table 1). *Drosophila* are readily accepted by many spiders including linyphiids (Nentwig 1983), although they may not usually be caught in linyphiid webs (Turnbull 1960; Nentwig 1980). Orthopterans are part of the natural diet of both *Argiope* (Levi 1968; Robinson 1969; Robinson and Robinson 1970) and *Nephila* (Robinson and Mirick 1971), and *Nephila* readily accept *A. domestica* crickets as prey (Robinson and Mirick 1971).

Experimental procedure

Neriene readily built webs in the laboratory and we were able to standardize the time since their last meal and minimize environmental disturbances. It was not expedient to observe *Argiope* and *Nephila* under similar conditions because of the much larger size of their webs. Instead, we observed them in the field, which allowed us to observe more of their natural behaviour.

We lightly dropped prey on the spiders' webs, allowed them to capture it, and disturbed them after about 5 min of feeding (or at the capture site for *Argiope*) by touching the dorsum of their abdomen with the tip of a forceps until they retreated to a corner of their web. The site on the web where we disturbed the spiders was the "virtual hub" for *Neriene*, the site of prey capture for *Argiope*, and the hub for *Nephila*. We then removed the prey from the web. *Neriene* and *Nephila* remained on the corner of their webs where they retreated for some time before returning to the feeding site. *Argiope* returned directly to the hub. We noted the spiders' behaviour after we stole their prey.

Neriene

We collected adult female *Neriene* at the edge of forest and pasture near Blaubeuren, Baden-Württemberg, Germany. We kept them in 10 × 10 × 5 cm plastic boxes containing wet napkins and small dry branches, and covered by plastic kitchen wrap, to which the spiders did not attach silk threads. We only used spiders that built webs 1–3 days after capture. To standardize the time since their last meal, we fed the spiders one *Drosophila funebris* fly as soon as they built a web capable of catching prey. If they did not feed on the 1st day, we offered them another fly once a day for 2 days. We only used spiders that fed in one of the three attempts. Then we kept the spiders for 1 day without food before beginning the experiment.

We used spiders only once and assigned them randomly to one of five experimental groups:

1. Spiders given a large prey, allowed to settle into feeding for about 5 min, and then disturbed and had their prey stolen ($n = 29$, 6 recorded on video with a Sony Video 8 Handycam).
2. Same as group 1 but with small prey ($n = 34$, 11 on video).
3. Same as group 1 but we replaced the prey in another part of the web ($n = 32$). This group served to evaluate the effect of disturbance on the web and how quickly spiders would find a prey that simply changed places in the web.

The following groups also served to evaluate the effect of disturbance on the web:

Table 1 Large and small prey used for each spider species. Prey sizes are given as mean ± SE

Spider	Large prey	Small prey
Neriene (Body length ~ 5 mm)	*Drosophila funebris* 1.08 ± 0.01 mm, $n = 30^a$	*D. melanogaster* 0.80 ± 0.01 mm, $n = 30^a$
Argiope (Body length ~ 4 cm)	Adult orthopterans 3.0 ± 0.3 cm, $n = 51^b$	Early instars of the orthopterans 0.8 ± 0.1 cm, $n = 51^b$
Nephila (Body length ~ 5 cm)	Adult *Acheta domestica* crickets 1.9 ± 0.1 cm, $n = 32^b$	Early instars of *A. domestica* 1.0 ± 0.1 cm, $n = 30^b$

[a] *Drosophila* thorax width measured with an optical grid attached to a dissecting microscope

[b] *A. domestica* and orthopteran body length measured to the nearest mm with a ruler

4. We disturbed the spiders as before, but did not steal the large prey we had given them. Instead we pulled on the web once with the forceps, next to the prey, to mimic the stimulus of stealing the prey with the forceps and to leave a hole in the web as if we had stolen the prey (*n* = 14).

5. We disturbed spiders that had received no prey (*n* = 18, 10 on video). We ended observation when the spiders had remained still for 30 min (*n* = 120) or walked out of the box (*n* = 7).

Argiope

We observed adult and penultimate-instar *Argiope* females in the field at Golfito, Puntarenas Province, Costa Rica. To each of 51 spiders we gave one large and one small prey, alternating between individuals whether the large prey was first or second. The period between trials for each spider was about two weeks. The spiders were studied in an open, pasture-like environment, where most had webs in isolated ground-dwelling bromeliad plants. There were few spiders per plant, so basic body size was enough for individual identification. Mature female *Argiope* change sites infrequently (Robinson and Robinson 1970).

We disturbed the spiders during prey attack and wrapping at the capture site (Robinson 1969) and stole the prey by cutting with scissors the radii to which it was stuck. We held the prey with a forceps during the procedure to minimize disturbance. Observation started when spiders began searching and ended when they resumed the resting position at the hub, the “cruciform attitude” as described by Robinson (1969). After the spiders resumed the cruciform attitude they did not move or respond to wind or to being blown upon. We counted the number of *Argyrodes* (Araneae: Theridiidae) kleptoparasitic spiders (Vollrath 1979a,1979b) on each web. To observe the spiders’ reaction to increased disturbance, we disturbed all spiders again after both trials were over by persistently moving a ruler near them without touching them.

Nephila

We observed adult and penultimate-instar *Nephila* females in the field at La Selva Biological Station, Costa Rica, and at Isla Bastimentos, Bocas del Toro, Panamá. We used each spider only once and randomly assigned it to one of five experimental groups. We gave the spider either:

1. Large (*n* = 8), or

2. Small (*n* = 6) prey, which we then stole by pulling the thread attaching it to the hub with a forceps.

There were three control groups:

3. Spiders observed without interference for 30 min to note their reactions to normal environmental disturbances like wind, prey, or plant debris falling on their webs (*n* = 12).

4. We disturbed spiders that had captured a large prey but did not steal it (*n* = 2).

5. We disturbed spiders that had no prey (*n* = 7).

The last two groups allowed us to see the effect of disturbance on the web. We stopped observation when the spiders had remained still for 30 min.

Results

Searching behaviour occurred in episodes interspersed with periods of quiescence. It was very different from behaviour observed at other times. *Neriene* walked around the web, softly plucking it with legs I and II. Sometimes they examined sticks in the box with their legs and mouthparts or walked along the rim of the box. *Argiope* and *Nephila* turned and walked around the orb, tugging on the web. *Nephila* also walked to the frames or barrier webbing. When spiders were allowed to find the prey *(Neriene)*, they stopped searching and resumed feeding. Thus, finding the prey appears to have been the object of searching. Spiders that captured large prey waited for a shorter time in their retreat and searched longer (Figs. 1, 2, 3). Detailed accounts follow.

Neriene

When disturbed, most spiders retreated and left their prey behind on the web. Of 43 spiders that captured large prey (combining groups 1 and 4), 30 left it behind, as did 25 of 34 that captured small prey. We report results from these spiders and discount those that retreated with the prey in their mouthparts. Sample sizes are: group 1 (*n* = 21), group 2 (*n* = 24), group 3 (*n* = 26), group 4 (*n* = 9) and group 5 (*n* = 18)

Spiders that captured prey waited for a shorter time in their retreat before returning than spiders disturbed without prey (Fig. 1). All spiders that captured prey searched (large and small prey, *n* = 21 and 24, respectively). In contrast, only 10 of 18 spiders disturbed without prey (group 5) searched ($G = 16.32$, $P < 0.001$). Searching time varied significantly between spiders that captured large, small, or no prey (Fig. 2).

In 24 cases, the web had remains of a fly the spiders had fed upon the day before the experiment (we did not remove them so as not to introduce additional disturbance into the experiment). Eight of nine spiders that searched for large prey and seven of ten spiders that searched for small prey examined the old fly, but none of the five control spiders that searched when disturbed without prey examined it ($G = 8.93$, calculated adding 1 to all categories, $P < 0.02$). Spiders that examined the old fly touched it with legs I and II, pedipalps, and mouthparts 1–12 times

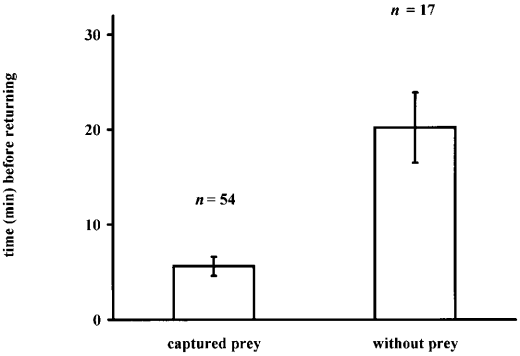

Fig. 1 Mean (± SE) return time for *Neriene* was significantly shorter when they had captured prey than when they had not (one-tailed $t_{69} = -6.15$, $P < 0.0001$, performed on $\log_{10}$-transformed data). Data for large (*n* = 29) and small (*n* = 25) prey were not significantly different (two-tailed $t_{52} = -0.24$, $P = 0.81$) and were pooled

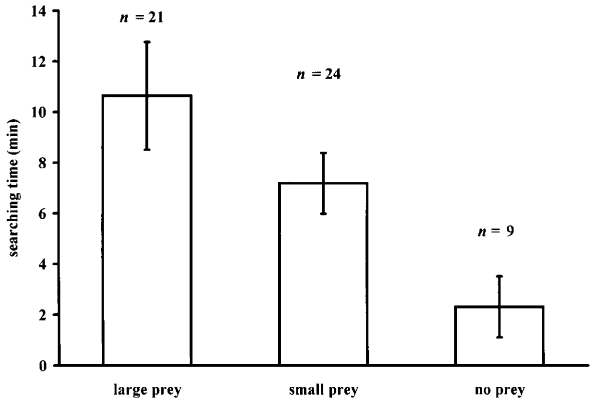

Fig. 2 Mean (± SE) searching time for *Neriene* was significantly longer when they captured large prey than when they captured small prey, which was longer than when they had no prey ($F_{2,51}$ = 9.12, $P < 0.001$, performed on $\log_{10}$-transformed data). We were unable to determine the searching time of one spider with small prey

for several seconds. None fed on it, presumably because it was already spent, and all continued searching afterwards.

Of 26 spiders whose prey we replaced in another part of the web (group 3), none located it immediately after returning, 19 found it after searching for 1.1 ± 0.4 min (mean ± SE), and 7 did not find it at all: they searched for 15.7 ± 5.1 min and then remained still for 30 min. Two of these walked within 0.5–1 cm of the prey several times in the course of searching but did not locate it.

Of nine control spiders which we disturbed but did not steal prey from (group 4), seven returned to the exact spot where the prey was and resumed feeding directly. The other two searched for 0. 9 and 4.3 min before finding the prey and settling into feeding. Then all fed for 30 min and we ended observation.

Argiope

Spiders that had captured large prey remained less time in their retreat than spiders that had small prey (Fig. 3). Of 51 spiders, 46 searched for large prey and 42 searched for small prey. They searched significantly longer for large prey (Fig. 3). The portion of the web covered (estimated as degrees of arc, with a maximum of 360° for the whole orb) and the number of times the spider tugged on the web whilst searching were significantly higher for large prey (Figs. 4, 5).

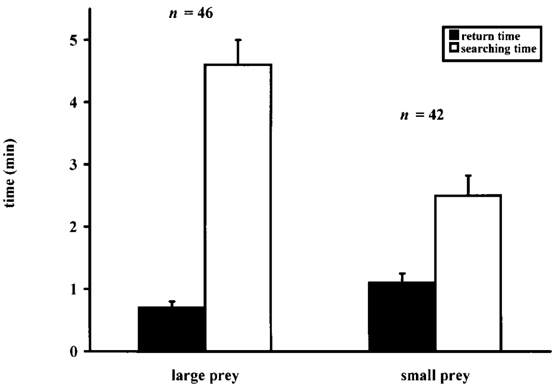

Fig. 3 When *Argiope* captured large prey, mean (± SE) return time was significantly shorter (one-tailed $t_{86} = -2.09$, $P = 0.02$, performed on $\log_{10}$-transformed data) and searching time was significantly longer (one-tailed $t_{86} = 4.13$, $P = 0.0001$)

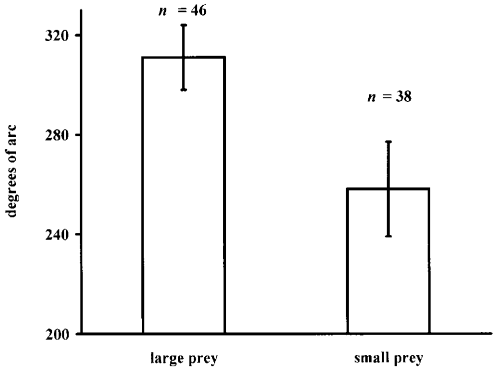

Fig. 4 *Argiope* searching for large prey covered a significantly larger portion of the web than spiders searching for small prey (one-tailed $t_{82} = 2.33$, $P = 0.012$, performed on $\log_{10}$-transformed data). Results shown are mean ± SE

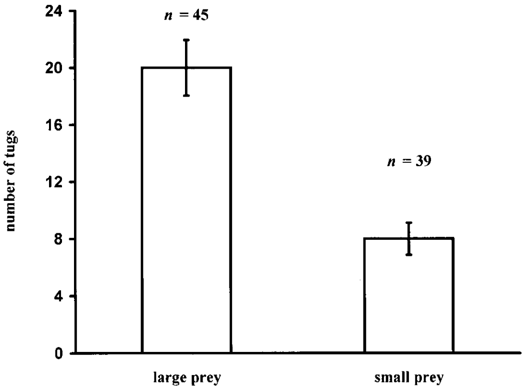

Fig. 5 *Argiope* searching for large prey tugged on the web significantly more times than spiders searching for small prey (one-tailed $t_{82} = 5.68$, $P < 0.0001$, performed on $\log_{10}$-transformed data). Results shown are mean ± SE

The number of *Argyrodes* kleptoparasites on the webs was not significantly correlated with searching time for either large (Pearson $r = -0.15$, $n = 46$, $P = 0.37$, performed on $\log_{10}$-transformed data) or small prey ($r = -0.03$, $n = 42$, $P = 0.87$, performed on $\log_{10}$-transformed data).

The behaviour of spiders disturbed further by moving a ruler near them did not resemble searching. Of 51 spiders, 10 responded by standing straight out on the web and pumping it with their legs, then shuttling from one side of the hub to the other without going around the orb. Two spiders defecated through the web towards the ruler. When further disturbed, they dropped from the web and hid among leaves near the ground.

Nephila

Nephila return time (mean ± SE = 1.6 ± 0.6 min, $n = 15$, pooling groups 1, 2 and 4) was not significantly different between spiders that had captured large (pooling groups 1 and 4) or small prey (two-tailed $t_{13} = -0.56$, $P = 0.24$, performed on $\log_{10}$-transformed data).

Seven of eight spiders that captured large prey and all six that captured small prey searched the web. They tended to search longer for large (mean ± SE = 3.3 ± 0.9 min) than for small prey (2.4 ± 0.6 min), but the difference was not significant (one-tailed $t_{11} = -0.36$, $P = 0.36$).

The behaviour of 12 spiders observed without disturbance (group 3) was different from searching. They responded to gusts of wind, prey, or plant debris by tugging only briefly and only in the direction of the stimulus. The two spiders we disturbed without taking their prey (group 4) resumed eating without searching. The seven spiders disturbed without prey (group 5) did not search.

The large prey of a spider was stolen by an *Argyrodes* kleptoparasite, which took it to the barrier webbing directly behind the hub. The spider searched with behaviour as described above for 5.8 min, did not seem to sense the *Argyrodes* or the prey, did not recover the prey, and then remained motionless on the hub for 30 min.

Discussion

In this study we tested whether the apparent searching behaviour of *Neriene*, *Argiope* and *Nephila* spiders was elicited by disturbance or some immediate stimulus that remained from the prey, whether it was indicative of memory of captured prey, and whether features of the prey were included in the spiders' memory. The evidence is limited in the case of *Nephila* because of the uncontrolled field conditions of our observations and the small sample size we obtained. But it is valid for contrasting searching behaviour with responses to disturbance, and it follows the same pattern as in *Neriene* and *Argiope*.

The hypothesis that searching behaviour was elicited by the disturbance we generated with our manipulations is not supported by the data. For *Neriene*, significantly fewer spiders from group 5 (disturbed without prey) searched. The searching behaviour of *Argiope* was different from their response to disturbance without prey, which instead resembled the defensive behaviour of *Argiope appensa* against web-invading predatory spiders. When disturbed experimentally or by predatory spiders, *A. appensa* pump and tug on the web, shuttle from one side of the web to the other, and sometimes drop from it (Jackson 1992; Jackson et al. 1993). Similar defensive movements occur in *A. aurantia* and *A. trifasciata* (Tolbert 1975; Hoffmaster 1982). Searching in *Nephila* did not occur at all unless their prey was stolen, and it was very different from the response to natural disturbances. Thus, all three species in this study performed searching behaviour for prey stolen from them.

The hypothesis that searching was triggered by immediate cues remaining on the webs, such as remnants of the taste or odour of the prey, or holes left in the web after stealing the prey, is also not supported by the data. Taste remnants are not likely because we removed the prey with its silk wrapping or, for *Neriene* and *Argiope*, with the bit of web on which it lay so that a small hole was left behind. Odour remnants may have dispersed somewhat by the time spiders returned, but this possibility is harder to rule out. Two trends argue against both of these explanations. First, when we moved prey to another part of the web, all *Neriene* searched, none immediately homed in on the prey, and some were not able to find it even after walking very close by several times. Similar results have been found for *Cupiennius salei* (Ctenidae): when they were disturbed and their prey moved to a different position on a solid surface, they did not react to it even when within 1 cm and only found it if they touched it while returning to the capture site (Seyfarth and Barth 1972). Second, some *Neriene* that had an old fly in their web did not examine it, which suggests the presence of the old fly (and associated cues) was not the cause of searching. Thus, searching does not appear to have been elicited by taste or odour cues remaining on the web, neither did these cues seem to aid the spiders to locate prey that was replaced in another part of the web.

The effect of holes left on the web can be discounted for *Nephila*, because when we pulled on the thread that attached the prey to the hub, no hole was left in the web, although we may have stretched or in some other way altered the condition of the threads. However, holes in the web may have affected *Neriene* and *Argiope*. For *Neriene*, evidence suggests that this possibility was not a problem. In group 4 we disturbed the spiders, did not steal their prey, but did pull on the web once with the forceps to mimic the stimulus of stealing the prey and to leave a hole. Most spiders in this group did not search, but returned directly to the prey and resumed feeding. In group 3 we moved the prey to another part of the web, leaving a hole on the prey's initial position. Most spiders in this group searched until they found the prey and then resumed feeding, so that the time they spent searching was much less than that of spiders searching for stolen prey, although similar holes were present in both groups. We have no data to evaluate the effect of holes on *Argiope*. However, taken together our data strongly suggest that spiders searched because they had memories of having captured prey.

The hypothesis that the spiders remembered features of their prey is supported by the data. *Neriene* and *Argiope* returned sooner and searched longer for larger prey, and *Argiope* also moved more and covered a larger portion of the web. These results are not likely to be due to variation in the motivation of spiders to search (hungrier spiders returning sooner and searching longer). For *Neriene* we standardized the time since their last meal. We did not do this for *Argiope* and *Nephila*, but variation in motivation to search would be more likely to confuse the pattern we observed than to happen to fit with our assignment of prey size. The reaction of *Neriene* to old and fresh prey appears to have been influenced by whether or not fresh prey had been encountered recently. Encountering fresh prey apparently made the spiders expect to find fresh prey again, although this may be explained by the old prey being entirely spent. Thus the spiders seem to have formed an expectation of finding prey with certain features. A firmer demonstration would require showing that the searching behaviour of the spiders, including searching longer for larger prey, is not innate. But this is not a very parsimonious hypothesis, and it would require the peculiar coincidence that our arbitrary definition of what was large and small prey for each spider fitted with the proposed hardwired searching programme.

Memory of captured prey may be advantageous for web spiders in several contexts. Kleptoparasites such as those that afflict *Argiope* and *Nephila* may be detrimental, especially when prey are scarce (Vollrath 1979 a, 1984, 1987; Rypstra 1981; Grostal and Walter 1997; Higgins and Buskirk 1998), and searching may aid the spider to recover the prey (Vollrath 1979 a, 1984). However, spiders often appear unable to locate the kleptoparasites and stolen prey when they have gone beyond the orb web itself (Vollrath 1979 a, 1984, 1987; Rypstra 1981; this study). It is puzzling that the number of kleptoparasites on the web was not correlated with searching time in *Argiope* in the present study. But spiders appear to respond to kleptoparasites by relocating the web when they experience lower prey capture rates (Rypstra 1981; Grostal and Walter 1997), which may be a relatively long-term process and may not affect the more immediate problem of searching for stolen prey. Against this explanation is evidence that *Nephila* does not form long term memories of site quality or capture rates (Vollrath 1986). But there are other contexts in which memory of prey features might be advantageous. Prey might escape the spider's grasp but not clear the web, or wind or other disturbance might change the position of the prey. And it would be advantageous to search longer for more valuable (larger) prey. These and other factors may have contributed to the evolution of a relatively detailed memory of captured prey.

Reports indicative of cognitive abilities in spiders are taxonomically widespread, ranging from salticids and ctenids to araneoids, and they range broadly in content (Bartels and Baltzer 1928; Bartels 1929; Bays 1962; LeGuelte 1969, 1970; Barth and Seyfarth 1971; Seyfarth and Barth 1972; Hill 1979; Seyfarth et al. 1982; Görner and Claas 1985; Eberhard 1988; Ades 1989; Jackson and Wilcox 1993 a; Tarsitano and Jackson 1994, 1997; Punzo and Kukoyi 1997; Whitehouse 1997; Heiling and Herberstein 1999; Venner et al. 2000). Thus, the selective pressures favouring cognition in spiders appear to be widespread and not restricted to a particular lifestyle.

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