# Spider Behaviour

*Flexibility and Versatility*

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**CAMBRIDGE**
UNIVERSITY PRESS

# 9

# Plasticity, learning and cognition

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As is becoming increasingly clear, spiders are not entirely instinct driven and inflexible in their behaviour. Here we review evidence for behavioural plasticity, learning and other cognitive processes such as attentional priming and memory. We first examine these attributes in several natural contexts: predation, interactions with conspecifics and potential predators, and spatial navigation. Next we examine two somewhat more artificial experimental approaches, heat aversion and rearing in enriched versus impoverished environments. We briefly describe the neurobiological underpinnings of these behaviours. Finally, we point to areas where our knowledge gaps are greatest, and we offer advice for researchers beginning their own studies of spider learning.

## 9.1    Overview

The history of the study of spider learning parallels that of insect learning, but lags well behind. At the start of the twentieth century, the general view was that insect learning was generally guided by instinct, but a steady accumulation of data has transformed our view of the importance of learning in their daily lives (reviewed in Dukas, 2008). In spite of their tiny brains, insects are capable of learning a multitude of tasks related to foraging, anti-predatory behaviour, aggression, social interactions, courtship and mate choice (Dukas, 2008). The study of spider behaviour is undergoing a similar transformation. Beginning over a century ago, researchers have periodically delved into the question of whether spider behaviour is primarily instinctual or can be modified with experience. For example, Peckham and Peckham (1887) reported that

spiders initially dropped out of their webs when approached by a ringing tuning fork, but after repeated presentations they disregarded it. Despite that early beginning, spider learning and cognition was generally neglected until the last several decades, when it began to be addressed more systematically and with well-controlled experiments. Unfortunately, these are still far fewer in number than those on insects.

As there is some variation in how different authors use terminology, we begin by defining our terms. *Cognition* includes the processes by which animals acquire, store, process and act upon information from the environment. Thus, cognition encompasses processes such as attention and priming, perception, information processing and decision making, in addition to learning and memory (Shettleworth, 2001). *Learning* is a sustained change in behavioural performance resulting from a change in the cognitive representation of relationships between cues (Domjan, 2006). The terms cognition and learning do not require us to infer any level of consciousness (Shettleworth, 2001). We define *behavioural plasticity* as a change in an animal's behaviour over time or under different circumstances. Plasticity alone is not sufficient evidence of learning or any other cognitive process, as behaviours may change because of a variety of non-cognitive processes, including satiation (e.g. Bilde *et al.*, 2002, Chmiel *et al.*, 2000, Li, 2000), maturational differences (Edwards and Jackson, 1994, Kreiter and Wise, 1996), reproductive condition (Cross *et al.*, 2007a), or temporal shifts in the environment (Chien and Morse, 1998). Without experiments, it is generally difficult, if not impossible, to distinguish plasticity from learning. The spider literature offers numerous examples of behavioural plasticity where the underlying mechanism has not been identified, whereas in other cases learning has been clearly demonstrated.

In selecting studies for review, we omit those in which there is evidence of choice but not of behavioural plasticity (e.g. male spiders select larger over smaller females; Hoefler, 2008). We also omit studies in which plasticity has been documented but is very unlikely to have a cognitive component, such as the cessation of feeding prior to moult or the halt in the production of prey-capture webs when a male matures. At the risk of overlap with other chapters in this volume, we briefly describe studies where cognition seems likely to play a role in plasticity but has not yet been experimentally addressed, as these suggest promising areas for future research.

## 9.2 Predation

Of all the types of behavioural plasticity we review, plasticity in predatory behaviour is the most commonly studied. Successful prey capture is a

complex feat for spiders, regardless of whether they rely on webs or actively hunt. Prey quality and availability vary across time and space, so there is a clear selective advantage for animals that are capable of distinguishing between relevant and irrelevant information. Here we focus on how spiders select and capture prey, choose web or foraging sites, and modify their web designs. Predatory plasticity is addressed in more detail in Chapter 3 of this volume.

### 9.2.1    Prey choice and capture strategies

Most spider species consume a wide variety of prey, limited primarily by their ability to subdue it. Nonetheless, a number of species change their predatory behaviour over time or under specific circumstances.

#### Prey choice

Prey choice in spiders often appears to be based on simple rules of thumb that may vary across species. Spiders may distinguish prey from non-prey, or one type of prey from another, based on very particular cues (e.g. Harland and Jackson, 2000, 2001, 2002). Preference for prey may be based on cues such as size, quality and species of prey. For example, in choice tests, the web-building spider *Micrathena sagittata* (Araneidae) consistently prefers larger over smaller prey (Diaz-Fleischer, 2005). Conversely, the wandering spider *Loxosceles reclusa*, though rarely a scavenger in nature, prefers smaller dead prey over larger live prey, thereby minimising predation risk (Cramer, 2008).

Some species have innate preferences for particular prey types, but these preferences are sometimes malleable. For example, some species prefer ants and exhibit an ant-specific predatory behaviour, independent of previous experience (reviewed in Huseynov *et al.*, 2005). Although the jumping spider *Aelurillus muganicus* exhibits an innate ant preference in laboratory choice tests, the frequency of ant encounters in the field is limited, so ants only account for 20% of their natural diet (Huseynov *et al.*, 2005). The salticid *Aelurillus m-nigrum* expresses its innate ant preference only when the laboratory environment closely mimics its native sandy habitat (Huysenov *et al.*, 2008). Prey preferences may also disappear with food deprivation. For example, three myrmecophagic species of *Aelurillus* shift from attacking only ants to accepting both ants and insects (Li *et al.*, 1999), although three species of *Zenodorus* continue to prefer ants even after 21 days without feeding (Jackson and Li, 2001). Similarly, the preference of araneophagic spiders for spiders over insect prey also disappears as they grow hungrier (Jackson and Li, 1998, Li, 2000, Li *et al.*, 1997). Preference may also vary based on venom availability. When offered a choice between two types of cockroaches that differed in venom sensitivity, the hunting spider *Cupiennius salei* chooses the more vulnerable prey when its venom glands are

depleted, but expresses no preference when glands are full (Wullschleger and Nentwig, 2002).

In the examples above, we generally do not know whether experience affects plasticity. In other cases, we have direct evidence of the role of experience. The wolf spider *Hogna helluo* (Lycosidae) does not exhibit an a-priori prey preference, but preference can be induced after regular feeding of a single prey type (Persons and Rypstra, 2000). When fed either crickets or a smaller wolf spider (*Pardosa milvina*) twice per week for one month, *H. helluo* spends more time on substrates with chemical cues from familiar prey. Prey preference has also been induced in *Oxyopes salticus* (Oxyopidae) spiderlings (Punzo, 2002a, 2002b) and *Hogna carolinensis* spiderlings (Punzo and Preshkar, 2002), and this preference persists even after subsequent feedings on alternative prey. By maintaining a preference for prey based on positive recent experiences, spiders can minimise the risk of the unknown, particularly when there is a chance that novel prey may be poorer quality or even toxic (Toft, 1999).

Spiders can learn to associate a new odour with food (Patt and Pfannenstiel, 2008). The nectarivorous spider *Hibana futilis* (Anyphaenidae) does not normally respond to the odour of vanilla. When spiders were offered vanilla (in the terminology of classical conditioning, the conditioned stimulus) along with sugar solution (the unconditioned stimulus) in an artificial nectary, they learned to associate the vanilla scent with the reward in a single trial and retained this association for several hours.

Several species are capable of developing aversions to toxic and/or distasteful prey. One of the earliest reports of a thorough experiment on spider learning is from Bays (1962), who reported that five orb-web spiders (*Araneus diadematus*, Araneidae) were trained to associate prey quality with frequencies of a ringing tuning fork. First, a dead fly dipped in an aversive quinine solution was thrown in the web and made to vibrate with a tuning fork. Five minutes later, a glucose-dipped fly was presented, along with a tuning fork of a different frequency. After 15 trials, all five spiders 'regularly' bit the glucose fly but not the quinine fly. After further training, flies were replaced by tasteless glass, and all spiders bit the beads only when they were vibrated with the frequency associated with glucose-dipped prey. Although this work was based on a small sample size and the report omits some procedural details, the results are intriguing. To our knowledge, this study has not been replicated.

Typically, the stronger an aversive stimulus, the longer that avoidance learning persists and the more likely it will generalise to similar stimuli across different contexts (Domjan, 2006). Not surprisingly, naive wolf spiders (*Pardosa prativaga*, Lycosidae) fed on one low-quality aphid species develop generalised aversions to other aphid species after only a few trials, and the aversion persists

for several hours (Toft, 1997). In contrast, the wolf spider *Hogna carolinensis* (Lycosidae) generally avoids unpalatable buckeye caterpillars, but there is no evidence that their avoidance behaviour improves with learning (Theodoratus and Bowers, 1999).

As has been well documented in the psychology literature, animals may learn not only the primary association, such as between the appearance or odour of prey and its bad taste, but also the context in which the association occurs (Pearce and Bouton, 2001). The jumping spider *Phidippus princeps* (Salticidae) learns to decrease its attacks on unpalatable milkweed bugs over eight successive trials (Skow and Jakob, 2006). Spiders are more likely to retain their aversion when background cues, also called contextual cues, remain identical to those present during learning. When contextual cues change, spiders do not generalise their aversion and are more likely to resume attacking milkweed bugs (Figure 9.1). Perhaps the lack of generalisation occurs because the cost of making a mistake is small: spiders release the bugs before ingesting toxic chemicals. In a different experiment, *P. princeps* did not avoid vegetation cues that had been previously paired with unpalatable milkweed bugs, but did avoid those same cues when they had been paired with a stronger aversive stimulus of mild electrical shock (Skow, 2007).

Hunting animals may become more likely to detect prey species with which they have had experience. In some cases, this phenomenon is due to Pavlovian conditioning: the predator's repeated experiences with prey lead to an association between the prey's characteristics and a food reward (Hollis, 1982). In other cases, another cognitive process may be involved, that of selective attention. Animals are capable of perceiving a wide range of stimuli in different sensory modes, but at any given moment only a subset of these stimuli are relevant. Attention is the mechanism by which animals select what to respond to from moment to moment (Shettleworth, 1998). Attention can be primed by experience. For example, the araneophagic spider *Portia labiata* is more likely to find a prey spider in a testing arena after a single experience with a prey of the same type (Jackson and Li, 2004). The fact that the behavioural change comes after only a single experience suggests that *P. labiata* has formed a search image for particular optical cues (Jackson and Li, 2004).

An even more compelling case for a role for selective attention comes from cross-modal priming, where experience with one cue heightens the response to another cue. The salticid *Evarcha culicivora* prefers to feed upon mosquitoes that have had a blood meal. Cross and Jackson (2009a) tested whether the presence of the odour of blood-carrying mosquitoes primes spiders to detect mosquitoes using visual cues. Test spiders were reared on lake flies and had never encountered a mosquito or its odour. Mosquito lures were made by mounting a dead
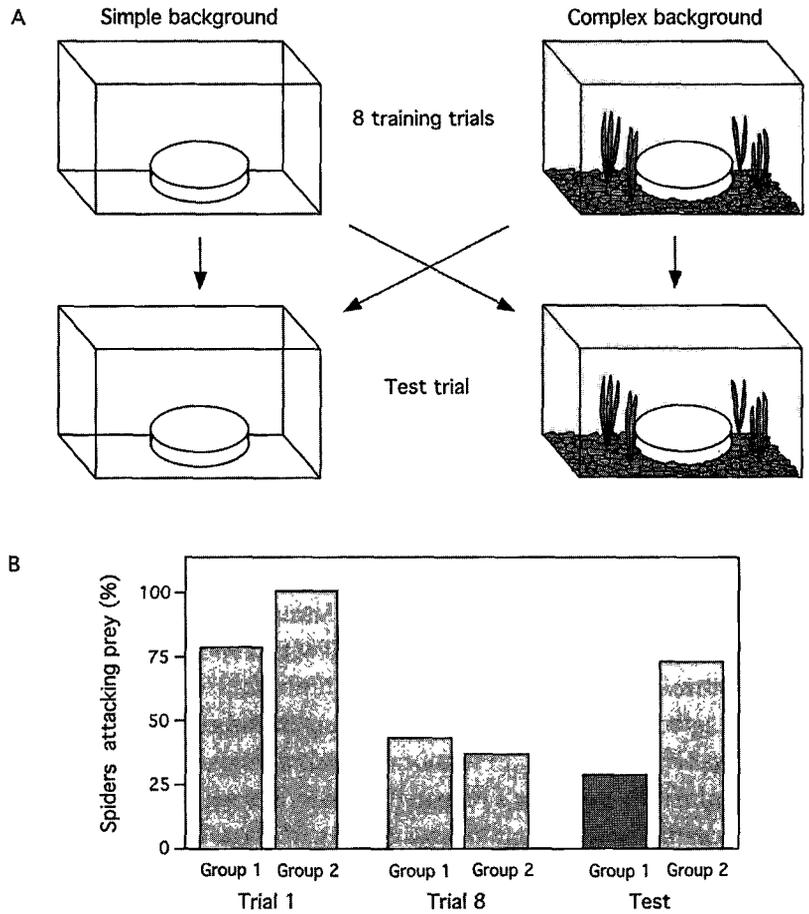
**Figure 9.1** (A) Experimental design to test for the role of contextual cues (different visual backgrounds) in learning to avoid toxic prey. (B) After learning not to attack distasteful prey, spiders tested with a new background resumed attacking prey, but spiders tested with a familiar background did not attack prey. (From Skow and Jakob, 2006, with kind permission from Oxford University Press.)

mosquito on a cork and spraying it with plastic adhesive to remove odour cues. When mosquito lures were conspicuous, spiders primed with odour were no more successful at detecting lures than were spiders that were not primed. However, when mosquito lures were made cryptic by including distractors and by covering the lures with nylon netting, spiders were more likely to find the lure when they were exposed to the scent of a blood-carrying mosquito. These results suggest that the odour had 'called up' an innate search image for the prey (Cross and Jackson, 2009a). Similarly, *Portia fimbriata* more quickly detected optical cues from its prey, the salticid *Jacksonoides queenslandicus*, after

exposure to chemicals in its dragline, even though *P. fimbriata* had no experience in capturing the prey (Jackson *et al.*, 2002a). For a complete discussion of attention, search images, and priming in spiders, see Cross and Jackson (2006).

### Capture strategies

Attack strategies may also be plastic. Some strategies change with age and size: for example, in the myrmecophagic spider *Aphantochilus rogersi* (Thomisidae), smaller spiders can only get a grip on an ant's petiole if they attack from the front, whereas older, larger spiders shift to attacking from behind (Castanho and Oliveira, 1997). Spiders may improve their prey-capture technique with experience. Several studies have shown that the attack success of spiderlings increases over repeated trials (Edwards and Jackson, 1994, Forster, 1977). With experience, crab spiders (*Misumena vatia*, Thomisidae) change the location of their strikes on prey (Morse, 1991), and orient to prey more rapidly (Morse, 2000a). Finally, naive *Nephila clavipes* (Nephilidae) are more likely to throw silk at a novel prey (stingless bees), but with repeated experience use a biting attack (Higgins, 2008).

Attack strategies may also change with energy state. For example, in the kleptoparasitic spider *Argyrodes flavescens* (Theridiidae), invaders use a host's web for prey capture, but the size of prey stolen from the web depends upon hunger levels (Koh and Li, 2003). Hungry invaders are more likely to either steal small prey or co-feed with the host on a larger prey item caught by the host, whereas well-fed invaders prefer to feed independently from the host.

The best-known work on flexible attack strategies comes from araneophagic salticids. Four genera (*Brettus*, *Cocalus*, *Cyrba* and *Portia*) all engage in 'cognitive smokescreen' behaviour during web invasions (Cerveira *et al.*, 2003). *Portia fimbriata* produces a series of signals, ranging from accurate mimicry of trapped insects to larger random disturbances in an effort to conceal its approach towards the host spider (Clark and Jackson, 2000, Tarsitano *et al.*, 2000). *Portia* can also take advantage of vibrations produced when the host spider is capturing prey to stealthily mask its own advances (Jackson *et al.*, 2002b). Initially, the invading *Portia* broadcasts a wide array of signals, but narrows its signal over time based on the behaviour of the host spider. This change in behaviour is evidence of trial-and-error learning (or operant conditioning) during web invasion (Jackson, 2002, Jackson and Wilcox, 1993a). Reliance on trial-and-error learning varies across lab-reared spiders derived from different populations of *P. labiata*, suggesting local adaptation to specific habitats. Spiders from areas with lower prey diversity exhibited far less reliance on trial-and-error learning than those from areas of higher prey diversity (Jackson and Carter, 2001). This pattern across populations supports the argument that innate predatory

behaviour (resulting in streamlined informational processing of specific stim-
uli) is favoured when environments remain stable over evolutionary time
whereas learning is more advantageous in unpredictable environments
(Japyassu and Caires, 2008, Japyassu and Viera, 2002).

### Retaining information about captured prey

Finally, spiders have also been shown to change their behaviour based
on the prey they have already captured and stored. Web-building spiders can
face concurrent feeding opportunities if prey items are snared simultaneously.
*Zygiella x-notata* (Araneidae) gain more energy from shorter feedings on multiple
prey versus prolonged feeding on one prey item (Sebrier and Krafft, 1993).
If *Zygiella x-notata* captures two prey items, it reduces its feeding duration on
the first prey, even if the second prey is removed from the web. This behav-
ioural change suggests that spiders retain information about the capture of the
second prey. Similar behaviour is demonstrated by the araneid *Argiope argentata*
(Ades, 1982).

### 9.2.2    Selection of web and foraging sites

Instead of actively searching for prey, many spiders wait for prey to
come to them. If foraging site quality is temporally autocorrelated and thus good
sites are likely to remain good over time, the ability to select good sites is likely
to increase fitness. Foraging success correlates with growth and egg production
in many species (e.g. Fritz and Morse, 1985, Vollrath, 1987). Sites may also differ
in other characteristics, such as the availability of web supports and the pres-
ence of predators.

A sit-and-wait predator has two decision points: the initial selection of a
hunting site, and the decision to abandon the site in search of a better one.
Both have been studied extensively, especially in web-building spiders. Webs
can be costly to produce. They are made of protein, which is frequently limited
in spiders' diets (reviewed in Blamires *et al.*, 2009). Web construction can divert
resources away from growth and development (Jakob, 1991). Even orb-web
spiders, which consume their webs and thus can recycle much of the raw
material (Peakall, 1971), must expend energy in the complicated movements
needed to construct a web (Venner *et al.*, 2003). All spiders, even those that do
not build webs, may incur lost-opportunity costs during a move (time spent
moving is time lost foraging; e.g. Morse and Fritz, 1982). Spiders may be more
vulnerable to predators during and after relocation (reviewed in Smith, 2009).
Thus, selecting a good foraging site prior to settlement should be advantageous.

Spiders can sometimes directly assess cues that indicate a high-quality site, as
a large literature attests. For example, web-building spiders select sites with

adequate space and anchorage points for webs (e.g. Lubin *et al.*, 1993), initiate web building more quickly when in the presence of conspecifics (Salomon, 2007), or build webs near artificial lights that also attract prey (Adams, 2000). Some species avoid chemical signatures left by predators (e.g. Persons and Uetz, 1996a, Rypstra *et al.*, 2007). Some can also detect prey cues. For example, in laboratory experiments, wolf spiders (*Schizocosa ocreata*) stay longer in patches that have chemical or visual cues of prey, even without food rewards (Persons and Uetz, 1996b, 1998). *Agelenopsis aperta* (Agelenidae) can choose web sites based on airborne vibrations generated by flies or by artificial means (Riechert, 1985). Crab spiders (*Misumena vatia*) wait for prey on flowers and attend to a variety of cues, including plant species, the quality of the bloom, and the presence of prey, even if they do not capture it (e.g. Chien and Morse 1998, Morse, 1988, 1993, 2000a).

Learning may modify the level of response to site quality cues. For example, Punzo (1997) compared the amount of time that wolf spiders (*Schizocosa avida*) spend on plain filter paper and filter paper that had come in contact with a scorpion, a voracious predator. Control spiders spent equivalent amounts of time on each substrate, whereas spiders that had escaped from a scorpion by autotomising a leg avoid the scorpion-scented paper. The behaviour of spiders with legs autotomised by the experimenter did not differ from control spiders.

Immediate cues of site quality may not always be available (e.g. Hoefler *et al.*, 2002), and spiders must instead sample a site in order to estimate its quality. Because of the stochastic nature of prey arrival, it would seem beneficial for a spider to remember its foraging experiences at a particular site. Indeed, Nakata *et al.* (2003) modelled the effect of memory on fitness, and predicted that spiders that have a longer memory window for their prey capture success in a particular site will make more accurate decisions about whether to abandon the site or stay. The effects of different costs of memory were not explored.

Although there are exceptions (e.g. Vollrath and Houston, 1986), numerous studies have shown that recent prey capture success influences a spider's decision to stay in a site. Many species apparently follow the rule of 'Win, stay; lose, shift', remaining in a site where they have captured prey, and moving on when they have not (reviewed in Jakob, 2004, Nakata *et al.*, 2003). However, although there may be a correlation between a spider's selection of a foraging site and its recent experience, it does not necessarily follow that a spider remembers its experience. Instead, it could be basing its decisions on its current hunger state. Nonetheless, some spiders do appear to have a short-term memory of prey capture: when experimenters stole captured prey from the webs of *Argiope argentata* (Araneidae), *Nephila clavipes* (Nephilidae) and *Neriene peltata* (Linyphiidae), spiders searched for the prey by walking around and pulling on

the web threads (Rodríguez and Gamboa, 2000). Spiders did not perform searching behaviour in response to artificial disturbance, nor did they home in on prey that were moved to a new section of the web. However, they did search longer for larger prey, suggesting that spiders were indeed looking for remembered prey.

We can get more insight into what a spider has learned about a site by experimentally manipulating a spider's foraging experience. For example, in the field, adult *Holocnemus pluchei* (Pholcidae) stay in webs longer when additional prey are added to the webs. A possible explanation is that spiders associate the presence of prey with a particular web site. However, a laboratory experiment demonstrated that this is not the case. When fed and starved spiders are moved to a new web, their decisions to leave or stay are based on their condition, even without the opportunity to sample prey availability at the new site (Jakob, 2004). Of course, when there is no experimental intervention, a spider's condition is likely to be correlated with its experience in a particular web, and thus condition can be a reliable indicator of site quality.

In another species, the effect of prey removal depended on how long spiders were in a site. Nakata and Ushimaru (1999) removed prey every three minutes throughout the foraging day from the orb webs of *Cyclosa argenteoalba* (Araneidae), wresting it out of the spiders' jaws when necessary. Spiders undergoing prey removal were more likely to move their webs the next day. This effect was particularly pronounced for spiders that had spent only a single day at the experimental site, suggesting that spiders incorporated both recent and earlier experience to determine whether to abandon a site. In contrast, neither prey capture nor prey cues experienced at a particular site influence subsequent visits to that site by the wolf spider *Schizocosa ocreata*, and Persons and Uetz (1997) suggest that learning is not important for this species in site selection.

Crab spiders (Thomisidae) select flowering plants on which to wait for prey. Morse's (2007) long-term studies of the foraging decisions of *Misumena vatia* suggest that the role of experience in site assessment increases as spiders grow. Spiderlings appear to have innate preferences for particular substrates, but older spiders show greater flexibility (Morse, 2000b, 2007). Older spiders select substrates similar to their immediately previous ones more frequently than expected by chance. Site fidelity is particularly strong if a spider moults on a particular flower type (Morse, 1999). Spiders that are shifted from milkweed, a good site, to rose, a poorer site, are more likely to leave the new site than were those moved to another plant of their accustomed species, suggesting that spiders remember their previous site from two days earlier and judge the new one accordingly (Morse, 2000c).

Another site characteristic that cannot be easily assessed prior to settlement is the possibility of web damage. When web damage is predictable, such as along paths used by mammals, relocation in response to damage will be beneficial. When the orb webs of *Argiope keyserlingi* (Araneidae) were experimentally damaged, spiders built new webs away from the direction of the damage (Chmiel *et al.*, 2000).

### 9.2.3    Web design

Spider web architecture varies not only across species, but across webs spun by a particular individual (see also Chapter 3). Sometimes, variation results from purely mechanistic constraints, such as available space, weather and spider growth (reviewed in Heiling and Herberstein, 2000). Some spiders vary their webs in response to more unusual environmental cues: for example, *Nephila clavipes* (Nephilidae) spiders change the colour of their silk in response to the spectral quality and light intensity in their environment, producing yellower webs when foraging in high light environments and thereby attracting bees (Craig *et al.*, 1996).

In some species, web size or structure depends on energy state. Orb-web spiders generally reduce investment in web building when satiated (reviewed in Venner *et al.*, 2000). In sheet-web spiders, the situation is more complicated because webs generally require more energy to construct and a starved spider may not have enough energy to build a web. In the linyphiid *Frontinellina* cf. *frutetorum*, spiders in better condition build larger webs, the opposite of most orb-web spiders. Western black widow spiders (*Latrodectus hesperus*, Theridiidae) modify both the amount of silk (Salomon, 2007) and the shape (Zevenbergen *et al.*, 2008) of their three-dimensional cob webs based on body condition. Webs built by starved western black widows are more effective traps because they contain more sticky gumfooted threads (Zevenbergen *et al.*, 2008).

As in the studies of choice of foraging site, it can be difficult to ascertain whether spiders with different feeding experiences build webs of different structures because of a memory of prey availability or simply because of internal cues about hunger state. Several experimenters have separated the effects of different aspects of the predation sequence on subsequent behaviour. For example, different groups of *Zygiella x-notata* (Araneidae) spiders were allowed to (a) detect prey that was then removed before the spider touched it; (b) capture prey and transport it to the retreat but not consume it; (c) complete the predation sequence; or (d) to feed on prey that they had not subdued themselves. Control spiders (e) were given no prey. The webs were then destroyed. During the next nocturnal period, spiders that had completed the entire predation sequence built smaller webs. Spiders that captured prey without feeding built

webs similar to those of spiders that had completed the predation sequence. There was no effect of prey detection alone on web construction. Spiders that were fed prey by hand delayed web building but did not modify the characteristics of their web. Thus, spiders used information gained during the act of prey capture to change the size and structure of the next web (Venner *et al.*, 2000).

Similarly, Nakata (2007) separated the experience of detecting prey from that of feeding on it by luring orb-web spiders *Cyclosa octotuberculata* with syrphid flies, but pulling the flies away before they were captured. Spiders that only sensed prey increased the total thread length and capture area of their webs relative to controls, but not as much as fed spiders, suggesting that both sensing and capturing prey provide information. In another study, only airborne vibrations of various types and density of prey were available to *Argiope keyserlingi* (Araneidae). Spiders were more likely to build webs when prey were present, but did not alter either the web size or mesh height of their orb (Herberstein *et al.*, 2000).

Orb webs are often asymmetrical, with the hub generally above the centre point. This design is thought to improve prey capture because the spider generally rests at the hub facing downward. Heiling and Herberstein (1999) noted that webs of older *Argiope keyserlingi* and *Larinioides sclopetarius* are more asymmetrical than those of juveniles. By depriving some spiders of the experience of building webs but controlling food intake by hand feeding, they found that spiders that are experienced with web building build more asymmetrical webs than those without experience. In addition, asymmetry increases when the lower portion of the web caught the most prey.

Besides amount of prey, the species of prey influences web structure in some species. *Parawixia bistriata* (Araneidae) build webs of fine mesh at sunset, capturing mainly small dipterans, but build webs of wide mesh during seasonal diurnal termite swarms (Sandoval, 1994). However, this behaviour is exhibited by spiderlings during their first encounter with termites, suggesting that it is not learned. *Parasteatoda tepidariorum* spin thicker and stronger threads when they had previously been fed crickets instead of less feisty pillbugs (Boutry and Blackledge, 2008).

Web architecture sometimes changes in the presence of predator cues. *Argiope versicolor*, like many other orb-web spiders, sometimes includes thick bands of silk called decorations or stabilimenta in its web. A number of functions have been proposed for stabilimenta, including prey attraction and predator defence. In *A. versicolor*, the stabilimentum has the unwanted side effect of attracting a visually hunting predatory spider, *Portia labiata* (Salticidae; Seah and Li, 2001). When exposed to odour cues from *P. labiata*, *A. versicolor* reduced stabilimentum area compared with groups exposed to no odour or the odour

of a non-predatory spider, *Lecauge decorata* (Araneidae; Li and Lee, 2004). In contrast, the odour of a praying mantid did not affect web-building behaviour in *Argiope keyserlingi* (Bruce and Herberstein, 2006). The role of learning in building decorations remains unknown.

## 9.3    Interactions with other animals

Here, we address behavioural plasticity in the contexts of agonistic, social and mating interactions, as well as anti-predator interactions. Spider communication is well studied and we touch on only a few highlights.

### 9.3.1    *Agonistic behaviour*

Spider contests can be costly, especially because losers are sometimes cannibalised. Thus, spiders that can adjust their fighting behaviour to behave more cautiously when warranted are likely to have a selective advantage. In spiders, contest duration, intensity and outcome are influenced by relative size of the combatants (e.g. Jakob, 1994, Taylor and Jackson, 2003), a cue that indicates the presence of a valuable resource (e.g. Cross and Jackson, 2009b, Cross *et al.*, 2006, 2007b, Jackson *et al.*, 2006, Wells, 1988), ownership of a resource (e.g. Hoefler 2002), and prior injury (e.g. Taylor and Jackson, 2003). Of particular interest to us is the role of experience in influencing contests. Whitehouse (1997) was first to document in a well-controlled experiment that previous experience influences spider contests. Male *Argyrodes antipodianus* of average size were paired. One spider was then repeatedly paired with larger combatants, and thus had the experience of losing. The other was similarly trained with smaller combatants, and thus trained to be a winner. Members of each pair were then matched against one another for the first time. Spiders trained as winners were more likely to continue to win. Similar effects of fighting experience have been found in other spider species, including crab spiders (Dodson and Schwaab, 2001, Hoefler, 2002) and jumping spiders (Kasumovic *et al.*, 2009).

Combatants may assess their chances of winning a fight by mutual assessment – that is, by assessing their own fighting ability relative to that of their opponent – or self-assessment, in which they determine only their own ability and fighting reserves. These two types of assessment generate different predictions about contest dynamics (Taylor and Elwood, 2003), so it is sometimes possible to distinguish between assessment modes (reviewed in Elias *et al.*, 2008). In an analysis of repeated contests with the same opponent in the jumping spider *Phidippus clarus*, Elias *et al.* (2008) suggest that contest duration is primarily driven by self-assessment, with a secondary role for mutual assessment. As in other species, losing males decrease aggression in subsequent fights.

While the physiological underpinnings of aggressive behaviour in insects are now becoming better understood (e.g. Hoyer *et al.*, 2008, Johnson *et al.*, 2009), only a little is known about the physiological response to aggression in spiders (see Section 9.7). However, the jumping spider *Portia labiata* can distinguish between the draglines of conspecifics that have lost fights versus those that have won fights (Clark *et al.*, 1999), implying that a physiological change brought on by fighting leads to chemical differences in their silk.

### 9.3.2    *Social behaviour*

Less than 1% of described spider species show some level of sociality (Uetz and Hieber, 1997). In a number of species, the tendency to form groups varies across populations, generally in those that face different ecological conditions. Common-garden experiments in which individuals from different populations are exposed to the same conditions enable us to ascertain whether the tendency to exhibit social behaviour is predominantly influenced by genetics (e.g. Cangialosi and Uetz, 1987) or the environment. For example, populations of *Parawixia bistriata* from dry habitats show plasticity for group capture of prey, whereas populations from wet habitats did not (Fernández Campón, 2008).

Variation in social behaviour can exist within a population, and even within a social group. For example, *Anelosimus studiosus* (Theridiidae) show two different behavioural phenotypes. 'Social' female spiders cooperate with other adult females in multifemale nests, react less aggressively to predatory cues and prey, and are less active. 'Asocial' females defend their nests against intrusions by adult conspecifics, and are more aggressive and active in other contexts as well (reviews in Pruitt and Riechert, 2009, Pruitt *et al.*, 2008). However, the role of experience in these two behavioural syndromes appears to be minimal (S. Riechert, personal communication). *Holocnemus pluchei*, the pholcid described in Section 9.2.2, joins and leaves groups depending on its size relative to other spiders in the group and on its energy state (Jakob, 1991, 2004), but whether its decisions are influenced by learning is unknown. In another species, the role of experience is clearer. Pourié and Trabalon (2001) forced a normally solitary agelenid, *Tegenaria atrica*, to live in groups after the period when they would normally disperse. Spiders in groups kept with few prey were likely to eat each other, but when prey was abundant, spiders built a communal prey-capture web and foraged in the same area. Thus, in social spiders there is ample evidence for variation in social tendencies, but the role of learning in influencing these tendencies is understudied.

*9.3.3    Mating behaviour*

Although many models of sexual selection assume that a female's preference is consistent (Andersson, 1994), female preference for male traits may in fact be plastic over the female's reproductive period. In spiders, female mating behaviour is influenced by female age (Uetz and Norton, 2007), female diet (Hebets *et al.*, 2008, Wilder and Rypstra, 2008a), and mating history (e.g. Cross *et al.*, 2007a). Male animals may also be choosy, especially when mating is rare and females vary in quality (Bonduriansky, 2001, Hoefler, 2008). In spiders, male choosiness may also change after mating (Gaskett *et al.*, 2004).

The role of experience with members of the opposite sex, separate from the physical act of mating, has been explicitly examined in several species. Several studies have shown that mating behaviours are influenced by what individuals experienced as juveniles. Fishing spider (*Dolomedes triton*, Pisauridae) females exposed, as juveniles, to a series of males were more likely to exhibit pre-copulatory cannibalism than were females that were not exposed to males. This may be because the exposure gives females a way to assess future mate availability, and thus alters the cost of sexual cannibalism (Johnson, 2005). Similarly, the mating behaviour of both male and female *Hogna helluo* (Lycosidae) depends on previous exposure to potential mates (Wilder and Rypstra, 2008b). Females exposed to males without mating were more likely to mate in a subsequent trial, whereas males showed the opposite pattern. Male choice may be acting in this species, so differences between the sexes may be due to the spiders' perceptions of mate availability and willingness to mate (Wilder and Rypstra, 2008b).

Juvenile experience also influences mate choice in *Schizocosa uetzi* (Lycosidae). In a single population, males vary in the amount of black pigmentation on the tibia of their forelegs. Hebets (2003) exposed penultimate females to males of a given phenotype, with forelegs painted either black or brown to mimic the extremes of the natural phenotypic spectrum. After maturity, females were then paired with males of either a familiar or unfamiliar phenotype. Females were more likely to mate with males of a familiar phenotype, and more likely to cannibalise males of an unfamiliar phenotype. This finding is especially interesting given that females were tested at least 11 days after their exposure treatment, and after they had undergone a moult, suggesting very long-term memory.

A different pattern is seen in another species. Hebets and Vink (2007) also examined *Schizocosa* from a mixed population composed of *S. ocreata*, in which males have forelegs ornamented with brushes, and *S. rovneri*, which are not ornamented. Here, females experienced with either brush-legged or

non-ornamented males are more likely to mate with brush-legged males upon maturity. Inexperienced females show no preference. Hebets and Vink suggest that experience with males may influence a female's perception of the availability and quality of potential mates, or possibly the female's perception of her own attractiveness.

There are limits to the effects of juvenile experience on mating preferences. Hebets (2007) examined whether subadult female experience with a sympatric heterospecific male could change mating preferences. Regardless of their exposure as juveniles, *Schizocosa uetzi* (Lycosidae) females were more likely to mate with conspecifics rather than *S. stridulans*, implying that species-specific cues override juvenile experience.

### 9.3.4    Anti-predator behaviour

Spiders respond to cues of their predators. We described in Section 9.2.3 how web architecture may change in the presence of predator cues. Hunting spiders also respond to cues from predators. A number of studies have examined the response of wolf spiders to chemical cues. The wolf spider *Pardosa milvina* reduces activity in the presence of chemical cues from a larger species, *Hogna helluo* (Persons and Rypstra, 2001), especially when the cues come from *Hogna* that had fed on *Pardosa* (Persons *et al.*, 2001). In these studies, field-caught *Pardosa* were used, so the role of learning cannot be evaluated. In another study, naive *Rabidosa rabida* wolf spiders that are exposed to chemical cues to a larger *Pardosa milvina* show more effective anti-predator responses to a live *Pardosa* (Eiben and Persons, 2007). The authors suggest that chemical cues may prime *Rabidosa* to be more attentive towards the predator, and that the response to chemical cues is unlikely to be learned. In contrast, as described in Section 9.2.2, an unpleasant encounter with a scorpion is necessary before *Schizocosa avida* avoids scorpion odour (Punzo, 1997). Thus, within this single family, we see a range in responses to chemical cues from innate to learned.

Courting animals are often at particular risk from predators. The araneophagic salticid *Portia fimbriata* is a predator of the salticid *Jacksonoides queenslandicus*, and prefers to eat females over males. Su and Li (2006) separated members of male and female pairs of *J. queenslandicus* with a clear barrier so that a male could court, but not reach, the female. Members of the pair then were exposed separately to a view of a predatory *Portia*. Male courtship frequency and duration was reduced when females could see the predator, but not when males could see it. Thus, the female's perception of risk most likely led to reduced responsiveness to the male, which in turn reduced his courtship effort (Su and Li, 2006).

## 9.4    Spatial learning and navigation

Spiders frequently face the challenge of finding their way back to a place they have been before, such as the location where they have left captured prey or the location of a prospective mate. In some cases, spiders can simply follow their own dragline back, but in a complex environment or over a long distance, this option is not available.

Navigation has been most extensively studied in wandering spiders that construct some sort of a retreat, such as a nest or a burrow. They then behave as central-place foragers, leaving the retreat on expeditions to find food or mates and then returning. Retreats are often very valuable resources, offering shelter during the night, in inclement weather, and when moulting, mating, ovipositing and guarding young (Jackson, 1979). They may be energetically expensive to construct, requiring an investment of both time and energy in the form of calorically rich silk or in digging out a suitable hole. Suitable places to construct retreats may also be difficult to find, and even if new sites are available, remaining in an area may bring benefits such as familiarity with the location of resources. For example, when the retreats of the salticid *Paraphidippus aurantius* were destroyed, spiders constructed new nests in the same locations as the old nests even though alternative sites appeared to be available (Mooney and Haloin, 2006). If spiders generally leave the immediate vicinity of their retreat, out of range of proximal cues emanating from it, then some form of memory must be used in order to locate it again. Web-building spiders may face similar problems, albeit over a smaller area. In the absence of odour or vibration cues, spiders might need to remember the location of a retreat or captured and quiescent prey.

Navigating animals may make use of local cues, such as landmarks or beacons, that indicate the location of the goal; the use of global cues, such as celestial or gravitational information, that indicate direction; or path integration, in which an animal keeps track of the direction and distance it has travelled from its starting point (reviewed in Healy, 1998, Wehner and Srinivasan, 2003). These mechanisms are not mutually exclusive (see Cheng *et al.*, 2009, for an example in which multiple strategies are employed). For instance, an animal may use path integration to return to the vicinity of its home, and then rely on local environmental cues for precise location. The use of a particular cue can often be demonstrated experimentally. For example, the araneid *Zygiella x-notata* captures prey on an orb web, and then returns to a nearby retreat to feed. If the web and retreat are flipped upside down when the spider is capturing prey, the spider initially runs in the original direction, and can only find its retreat after exploration (LeGuelte, 1969), suggesting that it uses gravity as a cue.

### 9.4.1    Landmarks and beacons

Animals may learn that some features of the environment, such as trees or rocks, may indicate the location of their retreat. Environmental features that are close to a goal are called beacons, while those that are further from the goal are landmarks. Intuitively, use of beacons is computationally less demanding than use of landmarks (Shettleworth, 1998).

The use of landmarks and beacons is relatively easy to confirm through experimental manipulation, as was famously demonstrated by Tinbergen and Kruyt's (1938) successful efforts to confuse digger wasps about the location of their nests by moving the surrounding pine cones. Hoefler and Jakob (2006) studied beacon use by the jumping spider *Phidippus clarus* in an overgrown field. By establishing a grid of potential retreat sites (plastic tubes) and individually marking spiders with bee tags, they demonstrated that spiders departed their retreats during the day and then returned to them at night. The role of beacon colour as a cue in locating retreats was then tested by placing nest tubes on dowels of different colours. Spiders colonised the tubes and constructed nests. Spiders were then captured from tubes, and released from a vial placed near a beacon. The first experiment tested three groups: naive spiders that were collected from a nest that did not have a nearby beacon; spiders collected from a nest on a beacon and released near that same familiar beacon; and spiders collected from a nest on a beacon and released near an unfamiliar beacon of the same colour but in a different location. The latter two groups were significantly more likely to approach the beacon than the naive spiders, but did not differ from each other. In a second experiment, all spiders were experienced with beacons, and were tested with a new beacon that was either the same colour as the beacon their nest had been on, or a beacon of a different colour. Spiders were significantly more likely to approach the beacon if it was the same colour as their own, even though other potential cues, such as the surrounding vegetation and the direction of the sun, were not available. Möller (2002) points out that picking out distinctive cues is the first step in landmark navigation, and these brightly coloured beacons against the green vegetation may have been noticeable to the spiders. Spiders in this genus are attracted to tall objects and are willing to cross gaps in order to reach them (Baker *et al.*, 2009), so they may have been predisposed to attend to these beacons.

Another spider that uses local cues to find its nest is *Leucorchestris arenicola* (Araneae, Sparassidae), a large species endemic to the Namib Desert, where it digs burrows into the sand. Because of lethal daytime temperatures on the sand's surface, these spiders are active only at night. Over long distances,

these spiders most likely use path-integration mechanisms, as described below, but use local cues when in the vicinity of their nests. Nørgaard *et al.* (2007) captured spiders foraging away from their burrows and displaced them by several metres, a distance too small for spiders to make reliable use of celestial cues. Ten of 12 spiders returned to their burrows. In contrast, when burrows themselves were displaced while spiders were away from them, only three of 15 spiders succeeded in finding them. Thus, spiders are not using odour cues emanating from the burrows, but rather may be using visual cues of the burrow's surroundings.

The jumping spider *Phidippus princeps* can also use beacons to find prey (Jakob *et al.*, 2007). Spiders were given a choice in a T-maze between a red and a blue cube. In training trials, a prey was secured behind a cube of a particular colour. Each spider was given four training trials followed by a probe trial with no prey present, and then a second set of four training trials followed by a probe trial. During the training trials, cubes were randomly assigned to different sides of the T-maze, so that only beacon colour but not its location indicated the location of prey. Spiders were allowed to explore the T-maze for an hour, but not all spiders successfully captured prey during the training trials. During probe trials, the first block chosen by the spider was scored. During the first probe trial (after four training trials) there was no evidence of learning. During the second probe trial (after eight training trials), there was a positive relationship between the number of successful training trials a spider had completed and its ability to correctly choose a block. This task was more difficult than situations that spiders are likely to encounter in nature, given that only colour and not location indicated the correct choice and that spiders were given only one trial per day.

### 9.4.2    Path integration

An animal using path integration (also known as dead reckoning) is able to take a circuitous outbound journey and then return directly to its starting point without retracing its path (reviewed in Wehner and Srinivasan, 2003). In order to do so, the animal continually updates its estimate of its position by monitoring the direction and distance of its travel and the angles of its turns. In spite of the apparent computational difficulty of this task, a number of arthropods, especially desert ants, are well known to be masters of path integration (e.g. Müller and Wehner 1988). While web-building spiders have also been shown to use path integration (e.g. Moller and Görner, 1994), here we focus on wandering spiders.

A typical test for the use of path integration is to capture an animal that is about to start a return journey to its home location and displace it to a new

location. An animal that is using path integration will search for its home location in a spot that is displaced by the same distance and in the same direction as the animal was from the location at which it was captured, whereas an animal that is relying on cues emanating from the home location should be able to find it again, as long as the displacement is not too large.

The wandering spider *Cupiennius salei* (Ctenidae) uses path integration to return to the site of captured prey after being chased away (Seyfarth *et al.*, 1982). To accomplish this task, *Cupiennius* uses idiothetic cues: it monitors its own body movements on the outbound path in order to keep an estimate of its location. Spiders gather information about their body position via lyriform organs, each consisting of a group of parallel slits in the exoskeleton that acts like a strain gauge: deformations in the slits when the animal moves excite nerve cells (Barth, 2002). The role of the lyriform organs in path integration was nicely demonstrated through ablation experiments (Seyfarth and Barth, 1972). Control spiders with intact lyriform organs were able to return to their nests, often in a straight line, whereas manipulated spiders with ablated lyriform organs were not.

The wolf spider *Lycosa tarantula* uses several sources of information during path integration. To measure turn angles, the spiders require visual input acquired through the anterior lateral eyes (Ortega-Escobar, 2006, and references therein). To measure distance travelled, *Lycosa tarantula* uses proprioceptive information (Reyes-Alcubilla *et al.*, 2009). Spiders that are chased away from their burrows can find them again, but those displaced passively in a clear container search near their release point, suggesting that active locomotion is necessary for spiders to estimate distances.

Path integration based solely on idiothetic (animal-centred) cues works only over short distances, because small errors quickly compound to make navigation imprecise (Benhamou *et al.*, 1990, Nørgaard, 2005). Over longer distances, accurate path integration must incorporate external cues for directional information, such as landmarks, celestial cues or magnetism. The desert spider *Leucorchestris arenicola* (Sparassidae), whose use of landmarks was described in the previous section, makes long journeys from the burrow (Henschel, 2002, Nørgaard, 2005), travelling a path as long as 810 m in a single night (Nørgaard, 2005). By masking different eyes with paint, Nørgaard *et al.* (2008) found that vision is necessary for navigation, even though these spiders are active only in darkness. Calculations reveal that the eyes are likely to employ spatial and temporal pooling in order to gain enough resolution to detect landscape structures. In lycosids and gnaphosids, the secondary eyes have evolved different mechanisms to detect the orientation of polarised light (Dacke *et al.*, 1999, 2001), a potential navigational cue.

### 9.4.3    *Detours and confinement tests*

Detouring is the ability to identify an alternative route to a reward when the direct route is blocked. The araneophagic salticid *Portia* can recognise prey on the basis of visual cues from as far as 30 cm away (Jackson and Blest, 1982), and is able to take long (>1 m) circuitous routes to reach potential prey in a web (Jackson and Wilcox, 1993b). These can be 'reverse-route' detours (Tarsitano and Jackson, 1994), in which the spider must turn away from the prey in order to reach it, and thus must hold a memory of the prey's location when the prey is out of sight. In the laboratory, *Portia* was presented with a prey lure visible from its starting platform, and a choice of routes that either led to the prey or did not. *Portia* can correctly select routes that required walking about 180° away from the lure and walking past where the incorrect route began (Tarsitano and Jackson, 1997), and can select complete routes over those with a gap (Tarsitano and Andrew, 1999; Figure 9.2). *Portia* appears to make its determination of which route to choose by following a simple set of rules: beginning at the lure, visually scan a potential route away from the lure along a horizontal feature, and if the potential route ends, turn back to the lure (Tarsitano and Andrew, 1999). When beginning in an open arena rather than a starting platform, *Portia* performs similarly, initially visually inspecting isolated objects but then switching to objects that are connected to the lure (Tarsitano, 2006). In these experiments, spiders were tested once, and did not learn to solve a problem through trial and error.

The detour behaviour of *Portia* can be flexible depending on the risk imposed by their prey. Spitting spiders in the genus *Scytodes* (Scytodidae) can spit sticky gum from their fangs. *Scytodes* and *Portia* co-occur only in some habitats (Jackson et al., 1998). Because *Scytodes* are dangerous prey, *Portia* will detour around to attack them from the rear. However, *Scytodes* carrying eggs are less dangerous – they are reluctant to drop their eggs but cannot spit when they are holding them, and *Portia* prefer them (Li and Jackson, 2003). When presented with an option to attack a scytodid by leaping directly at it or by taking a time-consuming but safer detour, *Portia* from populations that co-occur with scytodids adjust their predatory strategy based on whether the scytodid is holding eggs. *Portia* spiders chose a direct leap more often when the scytodid is holding eggs and presents less of a risk, and they detour more often when stalking eggless scytodids. In contrast, *Portia* from a population that does not co-occur with scytodids did not vary their approach (Jackson et al., 2002c).

In another design, Jackson et al. (2001) tested the role of trial-and-error learning in the ability of *Portia fimbriata* to solve a confinement problem: how to escape from an island surrounded by water. Two options were available: to leap
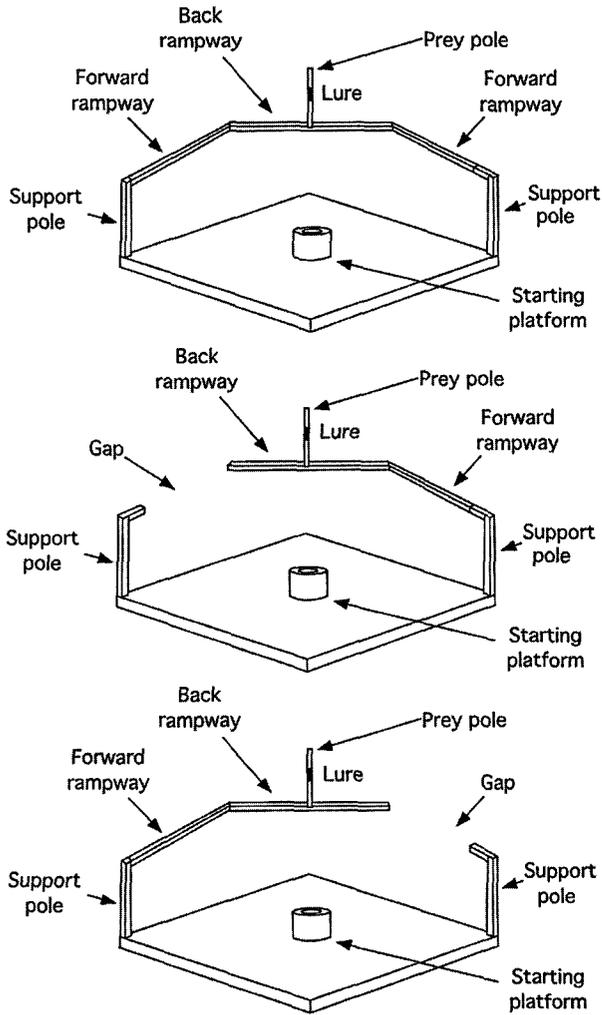
**Figure 9.2** Spiders can select the complete route before setting out. (From Tarsitano and Andrew, 1999, with kind permission from Elsevier.)

from the island towards an atoll (Figure 9.3), or to swim. The experimenters could reward either option by making small waves to push the spider towards the atoll, or could instead make waves to push the spider back towards the island. Once on the atoll or back on the island, the spider could make a second choice. From the atoll, it could choose to either swim or leap to reach the edge of the tray. From the island, it could choose again to either swim or leap to reach the atoll. Thus, the relationship between the success of the first choice and the second choice could be determined. Spiders that leaped first and were successful always leaped again. Spiders that leaped first but were preventing from reaching
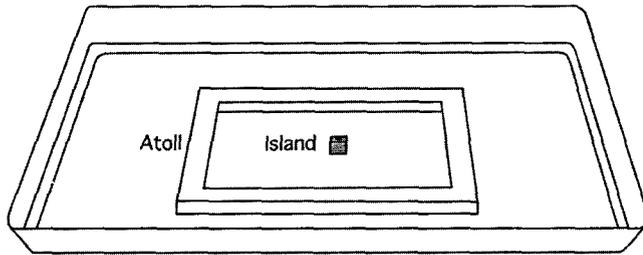
**Figure 9.3** Apparatus for testing the ability of salticids to solve a confinement problem. Spiders could leap or swim to reach the atoll from the island, and then leap or swim to reach the wall from the atoll. Spiders were more likely to use a strategy in their second choice if it was successful in their first choice. (From Jackson *et al.*, 2001.)

the atoll usually switched to swimming. Similarly, successful swimmers usually swam again in their second choice, and swimmers that failed in the first trial usually switched to leaping.

## 9.5    Heat aversion

Several groups of researchers have successfully trained jumping spiders to associate particular colours with an aversive level of heat. Nakamura and Yamashita (2000) were primarily interested in the ability of *Hasarius adansoni* to distinguish particular sets of colours. Spiders were placed in a small cylindrical arena, with floor and sides divided into two semicircles with different colours of papers. During training, half of the arena was heated from below. Spiders were given three three-minute sessions in the arena: no heat (control session), with heat, and again with no heat (test session). Immediately after training, spiders consistently avoided the colour associated with the heat during the test session (Figure 9.4). One day after training, spiders no longer discriminated between the two colours, suggesting that their memory of the association was lost.

VanderSal and Hebets (2007) used a similar procedure, but with a twist: they added a cross-modal cue. Spiders were exposed to a heat stimulus, as above. Some spiders, however, were simultaneously exposed to a seismic cue: a mini-shaker vibrated the arena during all trials. Other spiders were trained with only the heat stimulus. In a test trial with no heat, seismic-group spiders were more likely to avoid the previously heated colour than were non-seismic spiders. The authors suggest that the seismic stimulus may have increased the spiders' arousal or enhanced their attention to the visual cue.

In spite of their somewhat artificial nature, the simplicity of these experimental designs may offer a good tool for comparative studies of salticid abilities.
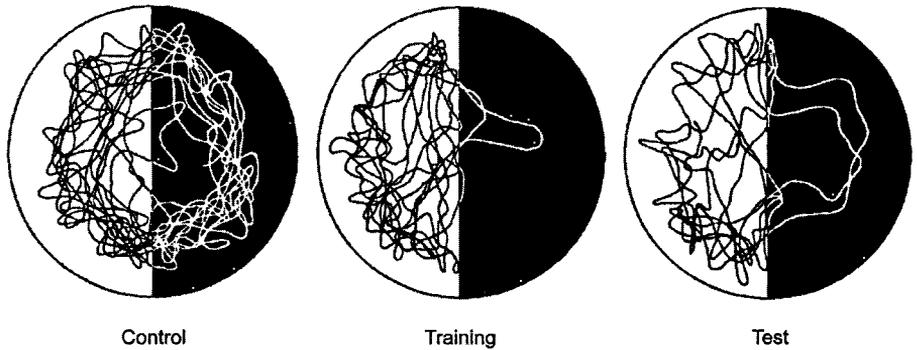
Control                    Training                    Test

**Figure 9.4** Path of a spider in control, training and test trials. In the control trial, the arena (60 mm in diameter) was unheated. In the training trial, the dark side was heated from the bottom. The test trial was in a new, unheated arena. Trials lasted for 3 minutes. (From Nakamura and Yamashita, 2000, with kind permission from Springer.)

For example, our research group (unpublished data) has not been able to replicate the Nakamura and Yamashita (2000) results with several species of *Phidippus*, even though we used colours that we know these spiders can distinguish. Further exploration of species-specific differences is warranted.

## 9.6    Environmental enrichment

To our knowledge, there are only two studies that show the effect of rearing conditions on the behaviour of spiders. Salticids (*Phidippus audax*) that were laboratory reared were less active in an open-field test, completed less of a reversed-route detour test, and were less likely to respond to videos of prey than were field-caught spiders. Behaviour was also affected by cage size and whether a green stick was provided in the cage (Carducci and Jakob, 2000). Wolf spiderlings (*Hogna carolinensis*) allowed to ride on their mothers' backs, as is normal, for 3 or 5 days were quicker to enter a novel arena than those that did not have this experience (Punzo and Alvarez, 2002). As described in the next section, in wolf spiders these differences are reflected in brain development.

## 9.7    The neurobiological basis of learning

We begin with a brief overview of the central nervous system (CNS) of spiders. A spider's CNS is divided into two regions, the suboesophageal and supraoesophageal masses, named for their position relative to the oesophagus (Barth, 2002, Foelix, 1996). The suboesophageal region is associated with the

nerves of the pedipalps and legs, the viscera, and non-visual sensory systems (Barth, 2002, Foelix, 1996). The supraoesophageal region comprises the cheliceral ganglia, which are associated with the chelicerae, fangs, and poison glands, as well as the protocerebrum (Barth, 2002, Foelix, 1996). For a discussion of the development and organisation of the neuromeres that compose these regions, as well as a comparison with other arthropods, see Scholtz and Edgecombe (2006). Within the protocerebrum, the third optic neuropils of the spider's eyes merge with other nerve tissue to form the visual-association centres (Barth, 2002). As far as is known, the protocerebrum receives direct sensory information only from the visual system, while the suboesophageal region receives direct information from all other sensory systems (Barth, 2002, Foelix, 1996). The protocerebrum and suboesophageal region are connected by longitudinal nerve tracts (Barth, 2002). While a major function of the protocerebrum is visual processing, connections between it and sensory and motor neurons in the suboesophageal mass raise interesting questions about its role in sensory integration and behaviour. In the context of learning and cognition, it is the area of most interest (Barth, 2002, Foelix, 1996).

Much of what we know about the neurobiology of spiders comes from the wandering spider *Cupiennius salei* (Barth, 2002). In *C. salei*, the protocerebrum is divided into two visual association centres, the mushroom bodies and the central body. The paired mushroom bodies accept visual input only from the secondary eyes, while the central body accepts input from both the secondary and principal eyes. In essence, then, visual information from the different eyes undergoes separate but parallel processing (Barth, 2002, Strausfeld and Barth, 1993, Strausfeld *et al.*, 1993).

The names for the mushroom bodies and the central body come from their superficial similarity to structures found in insects, crustaceans, myriapods and onychophorans (Strausfeld, 2009, Strausfeld and Barth, 1993, Strausfeld *et al.*, 1993, 1998), and indeed the structures in spiders were once thought to be homologous (reviewed in Barth, 2002). That hypothesis was challenged by comparative studies suggesting that the chelicerate protocerebrum is not homologous to its insect counterpart (Strausfeld and Barth, 1993, Strausfeld *et al.*, 1993, 2006), but additional studies at the level of gene expression are required.

Experimental manipulations of spider experience and its effect on brain structure have proved informative. For example, wolf spiderlings (*Hogna carolinensis*) allowed to remain with their mother and ride on her back with their siblings have larger protocerebrums, are able to capture prey more efficiently, and learn a maze task more easily than spiderlings raised in isolation (Punzo and Ludwig, 2002). These data indicate that spider brains are affected by the environment and continue to develop after hatching, and suggest that the

protocerebrum links to hunting ability, spatial learning and memory (Punzo and Ludwig, 2002), although other regions may also be involved in these behaviours.

Along with structural changes, neurochemical changes have also been linked to spider behaviour. Tarantulas (*Aphonopelma chalcodes*, Theraphosidae) that are trained to raise their legs to avoid a shock show decreased acetylcholinesterase (AchE) activity in their supraoesophageal region (Punzo, 1988a). Punzo (1983) suggests that decreases in AchE might be associated with memory consolidation. The spiders also showed significant increases in RNA and protein synthesis in both the central body and the mushroom bodies (Punzo, 1988a). RNA activity and protein synthesis has been shown to increase in the CNS of grasshoppers, *Schistocerca americana*, when they are subjected to a training regime similar to that of the tarantulas (Punzo, 1980). Tarantulas injected with cycloheximide, which inhibits protein synthesis, show impaired learning (Punzo, 1988a).

Neurochemical changes related to behaviour have also been studied in the tarantula *Aphonopelma hentzi* (Punzo and Punzo, 2001). Males exposed to antagonistic interactions with other males show decreased serotonin and octopamine in their supraoesophageal region compared with control males. The losers of fights show significantly lower levels of both serotonin and octopamine than do winners. Serotonin levels are depressed for up to 24 hours after the fight, while octopamine levels return to normal more rapidly. The complex role played by octopamine in arthropod aggression is still not well understood, and in *Drosophila*, its actions appear to be context dependent (reviewed in Hoyer et al., 2008). Other neurochemicals have been found in the brains of spiders, and much more work needs to be done to identify how these chemicals affect behaviour (Barth, 2002, Punzo, 1988b).

Many mysteries remain in our understanding of the function of the different brain regions and their relationship to behaviour. Arachnologists are somewhat limited in their experimental approaches because the hydrostatic pressure of spiders makes in vivo nerve recording or lesioning extremely difficult (but see Gronenberg, 1989, 1990). However, a large-scale, phylogenetically informed comparative study of brain region interconnectivity, neuronal density and neurochemistry may reveal correlations between behaviour and the brain and offer insights about the general patterns of brain organisation (as in Breidbach et al., 1995). Finally, additional experimental studies in which experience is manipulated and then brain morphology and biochemistry are examined would shed light on the neurological correlates of learning (as in Punzo, 1988a, Punzo and Ludwig, 2002, Punzo and Punzo, 2001). It would be particularly interesting to examine araneomorph spiders, as most manipulative neurochemical work has been done in mygalomorphs.

## 9.8    Conclusions and outlook

This volume illustrates the value of spiders as excellent organisms for the study of many larger questions in behaviour. This is especially the case for the study of learning and other cognitive processes, a field that offers many opportunities. The following areas are particularly ripe for exploration, and include both proximate and ultimate levels of analysis.

(1) *Neurobiological bases of behaviour.* Neurobiologists are not yet certain about which regions of the central nervous systems of spiders and insects are homologous or independently evolved. We should thus be particularly cautious about assuming that what we learn about the neurobiological basis of learning and cognition in insects applies to spiders. Mapping brain functions and additional studies of the neurochemical changes that underlie behavioural change are the next steps.

(2) *Characterising learning and memory.* Comparative psychologists have developed a battery of methods designed to test different aspects of learning and cognition (e.g. Shettleworth, 2009). Few studies of learning in spiders have explicitly examined fundamental properties of learning, such as how long spiders can remember tasks, and whether learning one task blocks the learning of another task. These questions are especially interesting to study in animals with small brains, as the extent to which brain size restricts the capacity to learn is unclear (e.g. Dukas, 2008).

(3) *Attention and priming.* Of current interest is how animals filter sensory information or are primed to attend to particular stimuli (e.g. Dukas, 2004a). Recent studies suggest that priming, even across sensory modalities (e.g. Cross and Jackson, 2006, 2010), might be a way that spiders direct their attention to what is important in their environment.

(4) *Fitness consequences of learning and cognition.* Throughout this review, we have tried to make it clear why learning or other cognitive processes might be beneficial in a particular context. However, few studies explicitly measure fitness benefits or costs of learning. Although by necessity many studies of learning and cognition must be carried out under controlled conditions, we should not lose sight of the selective forces acting on individuals in nature. Also neglected to date is a thorough investigation of individual differences in learning abilities and cognition (see Dukas, 2004b, for review). Recent work with *Drosophila* (reviewed in Kawecki, 2010) documents how quickly learning

may change in a population when genetic variation is present, and how the evolution of learning may have trade-offs. The presence of interpopulation variation in some of the behaviours we have described (e.g. Jackson *et al.*, 2002c) suggests that this will be a fruitful area of research.

(5) *Comparative studies.* The value of comparative studies in cognition have been amply demonstrated over the last 15 years or so, such as by exploring the correlation between the abilities of corvid species on learning tasks and their dependence on stored seeds (e.g. Balda and Kamil, 1998). The great diversity of spiders – from active hunters to web builders, from salticids with highly acute vision to those taxa that are essentially blind – offers opportunities for comparative studies of learning and cognition that have only begun to be explored. For example, there is tremendous variation even within families. The unusual araneophagic habits and complex environment of *Portia*, for example, may have led to its remarkable cognitive abilities (see Chapter 2). Carducci and Jakob (2000) tested detour behaviour in a much more typical salticid, *Phidippus audax*, with the same apparatus and experimental design that Tarsitano and Jackson (1994) used for *Portia*. Whereas *Portia* easily completed the detour, *P. audax* did not. Although these experiments were done at different times and in different labs and thus comparisons must be drawn with caution, the differences are intriguing. Coupling large-scale comparative analyses of behaviour with neurobiological studies may prove especially fruitful. Perhaps in a decade we will see advances as impressive as in the studies of mushroom bodies of insects (Farris, 2005).

We end our chapter with advice for researchers who may wish to study cognition and learning. Conversation with other arachnologists about their unpublished data, as well as our own experiences, suggests that there are many common experimental methods in animal learning that are very difficult to get to work with spiders. Careful experimental tests of learning require a negative or positive stimulus that can be consistently offered. In many learning studies, particularly in rodents, small bits of food are the usual reward in experiments using positive reinforcement. Selecting an appropriate food reward for spiders generates several difficulties as spiders are famously resistant to starvation (Foelix, 1996). However, even moderately food-deprived spiders can be enthusiastic predators. Spiders offered prey that are small relative to their body size made up to eight consecutive successful predatory attacks on different prey items (Skow and Jakob, 2006).

A second difficulty with food rewards is that many spider species do not detect, or refuse to eat, dead or immobile prey. Using live prey can be problematic because common experimental designs require a certain number of presentations of prey, and an uncooperative insect can mean discarding hard-won data. The use of small arenas, such as petri dishes, can mitigate this problem, but of course this means sacrificing a realistic environment. Where spatial location of the prey is important, it is sometimes possible to tether prey in place so that it can still make small movements (e.g. Jakob *et al.*, 2007). For spiders with good vision, such as lycosids and salticids, videotaped or computer-generated prey can provide a consistent stimulus (Clark and Uetz, 1990, Harland and Jackson, 2002). Of course, video prey do not provide any direct reward, but we have found that spiders persistently attack video images even in the absence of reward. Spiders can be motivated to escape from confinement (Jackson *et al.*, 2001). Finally, heat (e.g. Nakamura and Yamashita, 2000) or low-level foot shock (e.g. Skow, 2007) can be effective aversive stimuli. No method is foolproof or transferable to all species, so when embarking on research with a new spider species, it is essential to allow time for preliminary work in order to devise an appropriate training protocol.

## Acknowledgements

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