The capacity for spatial learning in spiders: a review

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Summary

Mobile animals must have an ability to orient and find their way around the environment. It can be said that the various types of spatial problems likely to be encountered by animals under natural conditions are relatively constant across species. A variety of tasks essential for survival, including the location of shelter, food, mates, and escape routes, are facilitated by navigational skills as well as spatial learning and memory. Most studies on spatial learning in arthropods have focused on insects, with less attention given to spiders. Spatial learning would enhance the ability of cursorial spiders to learn specific locations where prey may be more abundant, as well as locations of nests and escape routes. Web-building spiders utilise some aspects of spatial learning in assessing quality of web sites, and in forming memories of specific sites where prey has been captured in webs. Spiders use a combination of sensory cues, idiothetic and compass orientation, path integration, and landmarks when confronted with spatial tasks. The purpose of this paper is to review research that has shed some light on the capacity for navigation and spatial learning in spiders, and its adaptive significance.

Introduction

The survival of all mobile animals depends upon their ability to orient themselves in three-dimensional space (Able, 1991), and on their ability to navigate accurately throughout their habitats (Punzo & Chavez, 2003). Many animals accomplish this through various bodily movements and orientations (Turchin, 1991), homing behaviour (Papi, 1992), and spatial learning (Benhamou & Poucet, 1996).

Traditionally, the behaviour of arthropods had been viewed as almost entirely instinctive, characterised by relatively inflexible, genetically determined behavioural programs (Peckham & Peckham, 1887; Thorpe, 1963; Bitterman, 1975). More recent studies have not only shown that arthropods are capable of modifying behaviour based on past experience (learning) (see reviews by Rosenheim, 1993; Punzo, 1996; Menzel, 1999), but in addition, that some behaviours considered to be classic examples of instinct have modifiable components (Punzo & Garman, 1989; Punzo & Preshkar, 2002).

The ability of an animal to associate specific locations with the availability of some resource (spatial learning) has been shown to contribute to overall fitness in a wide array of animal taxa including insects, molluscs, and vertebrates (see reviews by Olton, 1978; Gallistel, 1990; Punzo, 1996; Holtzman, 1998; Lopez et al., 2001). For example, spatial learning ability can result in a significant decrease in time and energy allocated toward random searching movements in order to find food, thereby increasing the amount of energy available for other activities such as territoriality, courtship behaviour, and reproduction (Stephens & Krebs, 1986; Punzo, 2000).

Most studies on spatial learning in arthropods have focused on insects (see reviews by Papaj & Lewis, 1993; Beugnon et al., 1996; Punzo, 1985, 1996). Less attention has been given to spiders (Punzo, 2002a). Spatial learning would enhance the ability of cursorial spiders to learn specific locations where prey may be more abundant (LeGuelte, 1969; Punzo & Ludwig, 2002), as well as locations of nests and escape routes (Lahue, 1973). Web-building spiders may utilise some aspects of spatial learning in assessing quality of web sites (Vollrath & Houston, 1986; Nakata & Ushimaru, 1999), and forming memories of specific sites where prey has been captured in webs (Rodriguez & Gamboa, 2000). The purpose of this paper is to review research that has shed some light on the capacity for navigation and spatial learning in spiders, and its adaptive significance.

Acquired orientations, detour behaviour, and spatial memory

Mobile species frequently change their body orientation or actively move about their environment in order to optimise the utilisation of resources whose availability may change periodically (Ortega-Escobar, 2002). Movements that allow an animal to locate a shelter site or home are collectively characterised as homing behaviour (Mittelstaedt, 1983). A variety of homing mechanisms has been described (Papi, 1992).

One mechanism is known as path integration (Durier & Rivault, 1999). It has been shown that many animals often depart from a particular location to which they want to return and find their way back by keeping a record during their journey of the net distance and direction travelled from any starting point (Collett, 1993), thereby providing the animal with a continuous representation of its position in 3-dimensional space (Mittelstaedt & Mittelstaedt, 1980). In this way, a variety of environmental cues allows the animal to compare any current retinal images with a previously learned "cognitive map" associated with the goal (Cartwright, 1983). It allows an animal to relocate to some known location, such as a nest, without using exteroceptive spatial cues such as landmarks. Through path integration an animal can gauge and integrate angular changes in distance and direction by acquiring a vector trajectory whose length is related to distance travelled and whose orientation is related to home direction (Ortega-Escobar, 2002). Animals typically use information obtained from external cues including celestial polarised-light patterns or the position of the sun (Wehner, 1997), as well as proprioceptive information obtained from cuticular sense organs (Seyfarth et al., 1982; Mittelstaedt, 1983). Path integration has been described in funnel-web spiders (Moller & Görner, 1994) and wolf spiders (Ortega-Escobar & Muñoz-Cuevas, 1999), as well as insects, including ants (Wehner & Srinivasan, 1981; Ronacher & Wehner, 2000) and cockroaches (Durier & Rivault, 1999, 2000).

Some animals use another mechanism known as idiothetic orientation (Seyfarth *et al.*, 1982; Rovner, 1991). An animal's ability to organise behaviour with respect to spatial features may depend on the use of information obtained from external stimuli (allothetic orientation) or from internal sources (idiothetic orientation). The latter relies on the use of memorised information, associated with previous body orientations, when performing subsequent movements that utilise kinesthetic cues in helping animals to return to shelter sites as well as to lost or previously encountered prey (Görner, 1973; Mittelstaedt & Mittelstaedt, 1980). Kinesthetic cues are associated with the proprioceptive receptors that allow an animal to perceive orientations of various body parts as well as their rate of movement. For example, the funnel-web spider *Agelena labyrinthica* (Clerck) (Agelenidae) waits for suitable prey in the mouth of a silk funnel which serves as a retreat. When vibrating prey is caught in the web, the spider runs towards it, envenomates it, and carries it back to the retreat area where it is eaten. In performing these behavioural acts, *A. labyrinthica* uses both visual and kinesthetic cues (Görner, 1973).

Bartels (1929) was the first to report that the typically direct and linear path taken by *A. labyrinthica* when it returns to its retreat can be readily affected by the physical condition of the web. It is also affected by experimental manipulations, including changing the location of vibrational cues and the introduction of extraneous stimuli when an insect prey is first placed in the web. Under these conditions, spiders become disorientated and have difficulty finding the retreat. This behaviour seems to have both innate and learned components. There is an innate kinesthetic orientation ("Umdrehreflex") whereby the spider runs directly towards the entangled prey, grasps it, and then makes a 180° turn which results in a straight-line return to the retreat. However, with practice, the spider is also able to use the position of extraneous physical cues, such as flashing lights, to modulate this behaviour. Although earlier investigators considered this to be an example of a "learned orientation" (Görner, 1958; Lahue, 1973), it clearly demonstrates many of the characteristics of what is known as spatial navigation learning (Olton, 1978; Benhamou & Poucet, 1996; Punzo & Madragon, 2002).

Görner (1988) conducted a series of experiments on spatial memory in which adults of *A. labyrinthica* constructed webs between the walls of wooden boxes, allowing the assessment of the importance of optical cues in various orientation movements as well as the effects of the removal or alteration of these cues on subsequent behaviour. Experimental alteration of optical cues (by switching lights on or off) caused spiders to exhibit non-linear, random movements in their attempts to locate the retreat. When optical cues were moved to an opposite corner of the cage following several encounter sessions, the spiders frequently moved in a direction opposite to that of the retreat, suggesting spatial learning was involved in retreat location.

LeGuelte (1969) showed that there was a degree of plasticity associated with retreat orientation of a web-building spider, *Zygiella x-notata* (Clerck) (Araneidae).
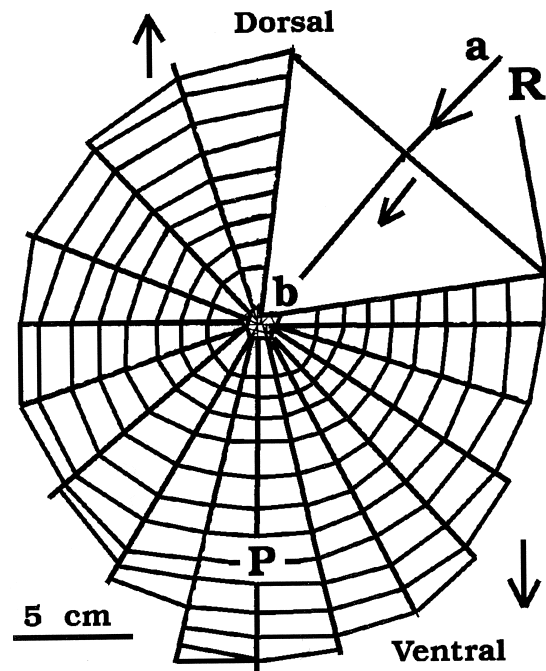

Fig. 1: Diagrammatic representation of the web of *Zygiella x-notata*. Locations on the web include: the hub, at the centre of the web (b), the retreat (R), and the site at which the prey item was entangled in the web (P). When a prey item becomes entangled in the web (P), the spider leaves its retreat (R) and runs along a single thread (a–b) until it reaches the hub, where it chooses a radial thread leading to the prey. It then uses the same path in reverse when returning to its retreat. If the web is rotated 180° (thereby changing the position of spatial cues), and the spider's web is presented with vibrations caused by a tuning fork, the spider rapidly locates the source of the vibration but becomes disorientated when returning to the retreat. The degree of disorientation decreases as a function of increasing number of practice trials. See text for further details.

A diagram of the web architecture of this spider is shown in Fig. 1. When a prey item becomes entangled (Fig. 1, P), the spider leaves its retreat (R) and runs along a single thread (a–b) until it reaches the hub at the centre of the web (b), where it chooses a radial thread leading to the prey. It then uses the same path in reverse when returning to its retreat. If the web was rotated 180° (thereby changing the spatial orientation of visual cues such as room windows), and the spider was presented with vibrations caused by a tuning fork, the spider rapidly located the source of vibration but became disorientated when returning to its retreat. The degree of disorientation, however, decreased significantly over a series of practice sessions as long as the intertrial interval was less than 4 hr, providing additional evidence that some degree of learning had occurred. In these experiments, the web position was reversed just before luring the spider from its retreat. Le Guelte (1969) suggested that information processed by the spider en route to the prey site may be used by the spider in its return to the retreat.

The occurrence of spatial memory is also exhibited by other web-building spiders. If a second prey item (fly) is placed in the web of *Araneus diadematus* Clerck (Araneidae) while it is feeding on a previously captured insect, it will leave the first prey item at the hub and then

rapidly move to the second insect (Peters, 1933). After wrapping it in silk, the spider returns to the previous prey, and the return route becomes more direct (linear) with increasing practice trials.

Jumping spiders (Salticidae) have the ability to remember the location of uncaptured prey (Tarsitano & Jackson, 1992). Many salticids make detour movements while pursuing visually-located prey when no direct route is available. They seem to form a spatial memory of its relative position, since they make frequent orientation movements that allow the spider to face the expected position of the prey. Detour behaviour is considered a form of spatial learning (Thorpe, 1963; Healy, 1995).

The wandering spider *Cupiennius salei* (Keyserling) (Ctenidae) is strictly nocturnal under natural conditions and appears to rely primarily on non-visual cues in orientation movements associated with locating shelter sites on agave and banana plants (Melchers, 1963). Following capture of prey, it wraps it in silk and attaches it to the foliage before ingestion. If it is disturbed during wrapping, it will temporarily leave the prey and then use idiothetic orientation to return to the capture site (Seyfarth, 1980). Seyfarth *et al.* (1982) showed that *C. salei* was able to memorise spatial information associated with its previous movements to locate lost prey. The degree of success in locating prey (as measured by the average distance transversed) declined linearly with increasing distance, suggesting that this spider has a limited capacity for idiothetic memory.

Punzo & Bottrell (2001) studied the ability of lynx spiders (*Oxyopes salticus* Hentz, Oxyopidae) to remember the location of an escape route when placed in an experimental chamber where they were exposed to a combination of aversive stimuli (bright light and high temperature). The floor of the square-shaped chamber contained 4 escape holes (Fig. 2, A–D). Each spider was placed in the middle of the floor (X) and allowed to move about until it located an open hole connected to an escape tunnel beneath the floor of the chamber, allowing the animal to escape the aversive stimuli. Spiders were randomly assigned to one of 4 groups depending on which of the 4 holes was open (the 3 remaining holes were covered with opaque plexiglass lids). The amount of time required to locate the open hole and the number of incorrect responses (contact with closed holes) were recorded for each trial. Results indicated that *O. salticus* has the ability to learn the location of an escape route. The amount of time required to locate a hole and the number of incorrect responses decreased significantly over a 5-day testing period. In addition, the actual paths taken to locate an open hole were random in earlier trials, but became increasingly more linear with increasing experience. The ability of an animal to learn the correct location of important resources including food, mates, and shelter sites would decrease random searching behaviour and contribute to its overall survival capacity.
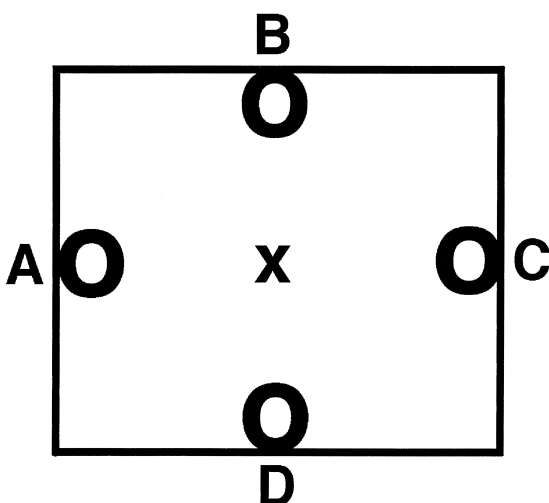

Fig. 2: Diagram showing dorsal view of the floor of the arena used to test spatial learning in *Oxyopes salticus*. Dimensions of the arena: 25 cm wide, 22 cm deep. Four holes (A, B, C and D), 4 cm in diam., were cut into the arena floor as shown. The spider was placed in the centre of the arena (X) facing hole B at the start of each trial.

Astronomical orientation

A number of species of *Arctosa* (Lycosidae) that are frequently found on land bordering water, possess an orienting ability that can direct them towards the shorelines of sandy beaches or river banks (Papi, 1955; Papi & Tongiorgi, 1963). They accomplish this by synchronising an endogenous physiological rhythm with the position of the sun. They orient themselves in such a way that if they come in contact with the water, they maintain a constant orientation toward the azimuth (magnetic north) that coincides with the most linear path towards the bank (Fig. 3, N). They use this as an escape path. On sunny days, spiders use the direction of the sun in choosing orientation angles; on overcast days, they orient visually using topographical features in their environment (Tongiorgi, 1962). This form of acquired orientation has been referred to as astronomical (Görner, 1964) or sun compass orientation (Lahoz-Beltra & Ortega, 1989).

Studies have shown that in the absence of cloud cover, *Arctosa cinerea* (Fabricius) orients itself on sandy beaches by using the plane of polarisation of light from a blue sky or the direction of the sun (Papi & Tongiorgi, 1963), and its body position changes at an angle that varies continuously over the course of a day. During testing (each test lasted 2 min), individual spiders were placed in a glass bowl divided into 16 sectors and filled to a depth of 5 mm with water. When placed on the water, the spiders began to move rapidly and bumped into the walls of the bowl in their attempts to escape. Each collision was considered an escape attempt, and the sector in which it occurred was recorded. The escape vector for each spider was observed and these vectors were used to determine r, the mean escape vector (Fig. 3). Bowl sectors were numbered clockwise with north (N) as zero. The direction of r was expressed in degrees and the length of r could vary from 0 to 1, with
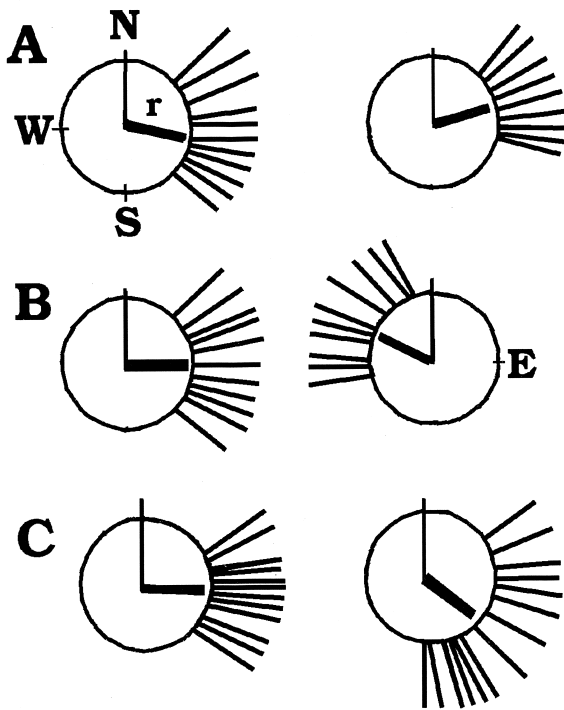
Fig. 3: Learning of escape direction in *Arctosa cinerea*. Compass directions indicated by north (N), south (S), east (E), and west (W). Diagrams (circles) indicate glass bowls used in experiments. The wide arrow inside each circle indicates the mean escape vector (*r*) for a group of spiders calculated from the vectors for individual spiders shown outside the circles. Circles on the left represent the initial (control) rearing conditions; those on the right, test sessions. The mean escape direction in each group was 90°. The theoretical escape direction in A remained at 90°, but was changed to 270° and 180° in B and C, respectively. See text for further details.

lower values associated with greater dispersion of escape attempts (Fig. 3).

All spiders (collected from different locations) exhibited a preference for a northerly-directed escape route within 30 days of hatching, whether they were reared from unhatched eggs collected from spiders in the field or from eggs deposited in captivity. Papi & Tongiorgi (1963) conducted a series of experiments using 3 groups of spiders with a theoretical escape direction of 90°. Spiders were maintained in bowls with water as described above. The escape direction was subsequently altered for 2 groups to 180° and 270°, respectively. After 15 days, most of the spiders from the 90° group continued to orient toward 90° (Fig. 3A), whereas the 270° group exhibited a marked shift in direction (Fig. 3B), and the 180° group did not exhibit an accurate shift in direction (Fig. 3C). However, after 15 days of additional trials, spiders from the 270° and 180° groups began to re-orient toward 90°.

On cloudy days, this spider orients itself visually by using objects or topographical features in its immediate environment, and will respond differently if these visual cues are manipulated. Some degree of spatial learning is involved, since it is capable of learning new escape routes (orientations) when escape direction is altered from an initial angle of 90° (to the shore) to 270°, and its ability to use visual cues improves with experience. In a similar way, the digger wasp *Philanthus triangulum*

learns to use localised visual cues to relocate its nest after capturing prey (Tinbergen, 1951); this has been described as having features of landmark learning as well as latent learning (Thorpe, 1963; Drickamer *et al.*, 2002).

Maze learning experiments

One way that spatial learning has been assessed in subjects from a wide array of animal taxa in the laboratory is through the use of simple mazes (T- and Y-mazes), as well as complex and radial mazes (see reviews by Alloway, 1972; Davey, 1989; Hodges, 1996). Mazes are valuable tools in studies on animal learning because they require test subjects to perform spatial tasks that have ecological relevance for mobile animals that actively search for food, nesting and shelter sites, and mates, as well as those that utilise escape routes (Punzo, 1988; Kimichi & Terkel, 2001; Punzo & Madragon, 2002).

In contrast to insects, few maze learning studies have been done on spiders. One of the earliest studies in spiders was conducted by Peckham & Peckham (1887) using the spider *Tetragnatha laboriosa* Hentz (Tetragnathidae). Adult males and females were able to learn to turn to the left or right in a Y-maze in order to avoid a noxious compound (oil of lavender) or to locate the source of food. The number of errors made by the linyphiid spider *Linyphia triangularis* (Clerck), trained to locate water in a T-maze, decreased significantly over a 10-day testing period (Thorpe, 1963).

Henton & Crawford (1966) conducted a series of experiments on the theraphosid spider *Aphonopelma californicum* (Ausserer) in a T-maze. Spiders were trained under 3 test conditions. In the first condition, half of the subjects in one group were trained under bright light with both arms of the maze uniformly illuminated, while the other half were trained using low (dim) light intensity. In both conditions, half of the spiders were initially required to turn left, and half to the right. In the second test condition, 4 groups of spiders were required to discriminate between multiple cues in the maze. A different group was trained to move to either a right-dim, right-bright, left-dim, or left-bright arm. In the third test condition, spiders were trained using polarised light (90° and 180°) instead of differences in light intensity as discrimination cues. Results showed an improvement in performance with experience: running times for all test groups decreased significantly over a period of 20 days.

In a more recent study, the jumping spider *Phidippus audax* (Hentz) (Salticidae) exhibited the ability to learn to make the correct turn in order to obtain prey in a T-maze, as well as to associate a coloured landmark with the presence of prey (Popson, 1999).

A study of reversal learning of a spatial task by adult males of the tarantula *Aphonopelma hentzi* (Girard) (Theraphosidae) was conducted by Punzo (2002a) using a simple T-maze. Subjects were required to choose the correct arm of the maze (which led to a darkened, insulated goal box) in order to avoid high ambient

temperatures produced by a light that was suspended over the centre of the maze. In an initial series of trials (first training session), subjects were trained to go to the right to reach the goal box. This was followed by a second series of training sessions in which the spiders now had to turn to the left (reversal training) to avoid the heat. Over 80% of the subjects reached the criterion for learning (14 out of 20 trials/day) after 11 days of training in the first training sessions, and 75% reached the criterion by day 12 in the reversal tests. This was the first demonstration of reversal learning in a theraphosid spider.

Males of *A. hentzi* were also tested by Punzo (2002a) in a complex maze with a floor plan similar to a maze originally used by Turner (1913) for experiments on cockroaches. It consisted of 6 blind alleys, a start box, and a goal box. Animals can be trained to run the maze to enter the goal box where they are rewarded with food or water (positive reinforcement), or are able to avoid aversive stimuli such as a mild electric shock, light, or heat (negative reinforcement). Each subject received 10 trials/day over a 14-day period. Over 70% of the subjects reached the criterion for learning (3 successive trials with <5 blind alley errors) by the tenth day of training. This was the first demonstration of complex maze learning for a theraphosid spider. Because sexually mature male theraphosids of the genus *Aphonopelma* are known to wander actively over the ground surface in search of burrowing females (Minch, 1977; Punzo & Henderson, 1999), any ability to learn and utilise spatial features of the environment might enhance their rate of success at finding females as well as food and shelter sites. This Turner maze has been used by subsequent investigators for maze learning experiments with other arthropods and vertebrates (Kimble, 1971; Bolles, 1975; Punzo, 2002b).

Using the Turner maze, Punzo (2002b) studied spatial learning in the wolf spider *Trochosa parthenus* (Chamberlin) (Lycosidae). This was the first demonstration of complex maze learning in a lycosid spider. This lycosid is an active hunter that typically wanders over the ground surface and leaf litter searching for prey (Gertsch, 1979). Individual non-gravid adult females of *T. parthenus* were placed in the start box and were required to run the maze and locate a goal box to avoid a mild electric shock. The number of blind alley errors decreased by 84% over an 8-day training period. In addition, the amount of time required to success-fully navigate the maze decreased by 80% over the same period of time. In contrast, control spiders that received a shock when entering the goal box showed no improvement in performance.

Similar results were reported for the lycosid spider *Hogna carolinensis* (Walckenaer) (Lycosidae) tested in a similar Turner maze (Punzo & Ludwig, 2002). Spiderlings were randomly assigned to 2 groups: an environmentally complex (EC) group, where spider-lings were allowed to remain in contact with their maternal parent and siblings after hatching, and an IC group (impoverished condition). In the IC group, egg sacs were removed from maternal parents, and after hatching the spiderlings were not allowed any contact with their mother or siblings. Although IC spiderlings demonstrated the capacity to learn the maze, EC subjects made significantly fewer blind alley errors as compared with their IC counterparts. This study was the first to show that early contact between lycosid spiderlings and their maternal parent and siblings can have a profound effect on their subsequent ability to learn spatial tasks.

The results obtained for *A. hentzi*, *T. parthenus* and *H. carolinensis* show that these spiders performed quite well in a relatively complex maze, with a level of performance similar to that reported for a number of other arthropods tested in mazes with similar floor plans, including decapod crustaceans (Punzo, 1985), cockroaches (Turner, 1913), thysanurans (Punzo, 1980), tenebrionid beetles (Alloway, 1972; Punzo & Malatesta, 1988), and ants (Schneirla, 1953; Alloway, 1973). They also show that some species of spiders can be useful subjects for maze studies that focus on trial-and-error spatial learning in terrestrial arthropods.

Discussion

Many arthropods typically find themselves in situations where they must move regularly from one location to another to capture prey (foraging), relocate food items, return to shelter and nest sites, or locate escape routes. It is clearly adaptive for an animal that actively searches for required resources to learn and remember the most efficient routes. To achieve this, animals must have the capacity to associate a particular site with its particular suite of available resources. This involves learning and remembering topographical features of the environment, as well as a range of specific navigational skills. Navigation, in a general sense, is a process whereby an animal determines and maintains a certain trajectory or pathway from one location to another, and includes choosing a direction towards a goal and some ability to estimate the distance required to reach it (Gallistel, 1990; Collett, 1993; Durier & Rivault, 2000).

The consolidation and processing of route-based information that is used by an animal to assess its position in 3-dimensional space are facilitated by the use of landmarks and other visual cues, olfactory cues, and path integration. In a general sense, path integration is the process whereby an animal can deduce its location from its previous movement/orientation patterns (Etienne *et al.*, 1988). As discussed previously, it enables a foraging animal to gauge and integrate angular changes related to direction and distance through acquired vector trajectories, resulting in a decrease in random search time required to relocate a nest, retreat, high quality feeding patches, or escape routes. Path integration has been reported for mammals (Etienne, 1992), several spiders including lycosids (Ortega-Escobar & Muñoz-Cuevas, 1999) and agelenids (Moller & Görner, 1994), as well as for cockroaches (Durier & Rivault, 1999, 2000) and ants (Ronacher & Wehner, 2000).

Spiders typically use webs, crevices, or burrows as places where they can ingest captured prey, deposit their egg sacs, escape from predators, and find shelter from unfavourable climatic conditions. Although some spiders are rather sedentary in nature, many others travel over considerable distances before selecting new locations in which to construct a web, dig a burrow, or find some suitable perch site. In some situations, suitable locations may be scarce and competition for them high, and the acquisition of suitable shelter and nest sites can determine whether an animal lives or dies. As a result, those individuals with an increased ability to learn and remember the location of these sites should have an advantage over those with a more limited capacity for spatial learning. Animals, including spiders, frequently remember specific sites in terms of the distance and direction from a known reference location such as specific topographical features (Able, 1991; Beugnon *et al.*, 1996), or extraneous visual (Görner, 1964; Papi, 1992) or chemical cues (Punzo & Kukoyi, 1997).

Foraging routes are characterised by outbound and inbound paths intermixed with varying numbers of transitional periods during which an animal makes decisions involving specific orientation movements. The studies discussed previously show that spiders exhibit a variety of orientation and navigation abilities, many of which have learned components, as well as the capacity to learn a variety of spatial tasks. These capabilities assist spiders in locating prey and decreasing the energy expended in finding food, shelter, potential mates, and escape routes. For example, cursorial spiders frequently leave their nests when searching for food, water, nest materials, or mates, and often concentrate their activities in areas where resources had been found previously (Persons, 1999). Males of many insects and spiders travel to particular sites because it increases the probability of encountering females which might be attracted to certain resources found there (Singer & Riechert, 1994; Collett, 1996) and that had been encountered by males on previous visits to those locations. After learning which sites are more likely to be visited by females, male spiders often become territorial and will defend these areas from incursion by other male competitors (Riechert, 1978). Similar findings have been reported for other web-building spiders when making decisions involved in finding suitable sites to relocate their webs following declining prey availability (Vollrath & Houston, 1986; Nakata & Ushimaru, 1999).

Spiders have the ability to store proprioceptive and external sensory input as memory and to retrieve this information at a later time in order to make decisions involving the orientation of their bodies in 3-dimensional space. Furthermore, some components of these orientations can be learned within a few seconds, as is exemplified by some web-building spiders that can remember the direct return route after a single run out from their retreat (Bartels, 1929; Görner, 1958; Moller & Görner, 1994). Similar results have been observed for burrowing spiders returning to their burrow entrances (Punzo & Henderson, 1999) and shore-dwelling spiders returning to shelter sites (Morse, 2002).

Research has also shown that experience and learning can play an important role in web-building behaviour (Vollrath, 1992). Heiling & Herberstein (1999) showed that older orb-weaving spiders (*Argiope keyserlingi* Karsch and *Larinioides sclopetarius* (Clerck), Araneidae), that had previous experience in web building, constructed webs that were more asymmetrical than conspecifics deprived of any building experience. Experienced spiders invested significantly more silk material in the area of the web below the hub. In addition, juvenile spiders constructed perfectly symmetrical webs, but after 30 days their webs were asymmetrical. As a result, the ventral region had a greater surface area for prey capture than the dorsal region. They suggested that web asymmetry may be associated with the cumulative effects of experience obtained throughout the development of the spider. This modification of web pattern based on experience resulted from the fact that spiders had intercepted significantly more prey in this region of the web over a 6-day period. Experienced spiders also spent more time exploring the web region below the hub, suggesting that they had formed some type of spatial memory of the area.

This lends support to earlier studies on the ability of web-building spiders to remember the location of previously captured prey items. For example, Peters (1969) showed that *Araneus diadematus* (Araneidae) can remember the specific location of a previously captured fly. After capturing a fly, another fly was introduced at a different location in the web. The spider typically left the first fly and rushed immediately to the site where the second fly was caught. After wrapping the second fly in silk, the spider used a direct linear path to return to the site of the first fly, even if the fly had been removed while the second insect was being secured. Jumping spiders of the genus *Phidippus* (Salticidae) may make detours when pursuing prey that they have located at a specific site. Although these detours often result in the spider losing visual contact with the prey for some period of time, these spiders appear to retain a spatial memory of the relative position of the prey at all times during the stalking sequence (Hill, 1979; Tarsitano & Jackson, 1992). Collectively, these studies indicate the capacity for spatial learning in spiders and how such an ability can facilitate the location and capture of prey.

In conclusion, mobile animals must have an ability to orient and find their way around the environment. It can be said that the various types of spatial problems likely to be encountered by animals under natural conditions are relatively constant across species. A variety of tasks, including the location of shelter, food, mates, and escape routes, are facilitated by spatial learning and memory. Although the majority of studies on spatial learning have been conducted on birds and mammals, representatives of several animal taxa including reptiles, fish, molluscs, and arthropods have demonstrated some capacity for this type of learning. Indeed, spatial learning ability is essential for the survival of most animals in their day-to-day search for required resources. Like other animals, spiders use a combination of sensory

cues, idiothetic and compass orientation, path integration, and landmarks when confronted with spatial tasks.

Acknowledgements

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