Spatial learning in the lynx spider *Oxyopes salticus* Hentz (Araneae, Oxyopidae)

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Summary

We investigated the spatial learning ability of the lynx spider *Oxyopes salticus*. Experiments were conducted in a square arena whose floor contained four escape holes located at the centre edge of each side. The arena was exposed to bright light and heat, establishing aversive conditions within its interior. Twenty spiders were randomly assigned to each of four test groups (G1–G4). For each group, only one specific hole was open, allowing individually tested spiders to escape the aversive conditions in the chamber by crawling down into an escape tube. Individual spiders were placed in the centre of the arena at the start of each trial, always facing in the same direction, and the following data recorded: amount of time required to locate the open hole, the number of incorrect responses (contact with closed holes), and the actual route (pathway) taken by the spider from its initial starting point to the open hole. Results indicated that *O. salticus* has the ability to learn the location of an escape route. The time required by spiders from all test groups to locate the open hole, as well as the number of incorrect responses, decreased significantly over the 5-day testing period. The pathways of spiders in initial trials were random, but by day 5 their routes to the open hole were much more direct. This is the first demonstration of spatial learning in an oxyopid spider.

Introduction

Learning is defined as a relatively permanent change in behaviour that occurs as the result of experience (Bitterman, 1975; Davey, 1989). The ability of an animal to learn foraging routes or to associate a specific location in three-dimensional space with the availability of food or shelter sites (spatial learning) can contribute significantly to its overall survivorship (Benhamou & Poucet, 1996; Biegler & Morris, 1996; Punzo, 2000a). Indeed, it has been argued that spatial learning is a necessary prerequisite for most animals to survive in their natural environments (Bitterman, 1975; Staddon, 1983). Most studies of spatial learning have been conducted on birds (Falk *et al.*, 1992; Willson & Wilkie, 1993; Clayton & Dickinson, 1998) and mammals (Olton, 1978; Gallistel, 1989; Able, 1991; Poucet, 1993; Janson, 1998), with fewer analyses available for fish (Reebs, 1994; Hughes & Blight, 1999) and reptiles (Holtzman *et al.*, 1999; Punzo, 2000a).

More recently, studies on spatial and spatio-temporal learning have been extended to arthropods, with the greatest attention focused on social insects. For example, some ants have demonstrated the ability to learn several associations between temporal and spatial changes in the daily pattern of food location and availability (Schatz *et al.*, 1999). Other insects show the capacity to discriminate, select, and store spatial information within several days, allowing them to locate

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specific sites where prey are abundant (Collett *et al.*, 1992; Lehrer & Collett, 1994; Beugnon *et al.*, 1996). Maze learning, a type of spatial learning task used by some investigators to study the ability of an animal to learn the most efficient foraging route (Punzo, 1980; Rosenheim, 1993), has been demonstrated in a number of insect species (see reviews by Schneirla, 1962; Thorpe, 1963; Alloway, 1973; Punzo, 1985, 1996).

Since spatial learning in arachnids has received far less attention (Punzo, 2000b), the present study was undertaken in order to assess the ability of *Oxyopes salticus* Hentz to learn the location of an escape route to avoid unfavourable environmental conditions (bright light and heat). To date, spatial learning has not been investigated in oxyopid spiders.

Methods

The spiders used in these experiments were adult, non-gravid females reared from hatchlings obtained from egg cases collected in Hillsborough County, Florida (USA), during July and August 1996. Spiderlings were housed separately in 500 ml glass containers and maintained at 21°C, 70% RH, and 12L:12D photoperiod regime in a Percival Model 80A (Boone, Iowa) environmental chamber. They were fed to maturity on a diet consisting of crickets (*Acheta domesticus*), mealworms (*Tenebrio molitor*), and apterous fruitflies (*Drosophila melanogaster*), and water was provided *ad libitum*. The mean body length of all females used in this study was 5.98 mm ($\pm$ 0.4 SD).

The arena (25 cm wide, 22 cm deep, and 15 cm high) used to test for spatial learning is shown in Fig. 1. It had a wooden floor with Plexiglass™ sides, and the entire interior was painted black with spray paint. Four holes (4 cm in diameter) were cut out of the bottom (floor) of the arena (Fig. 1, A–D). A 200-watt photographic white lamp was placed 35 cm above the floor of the arena. At
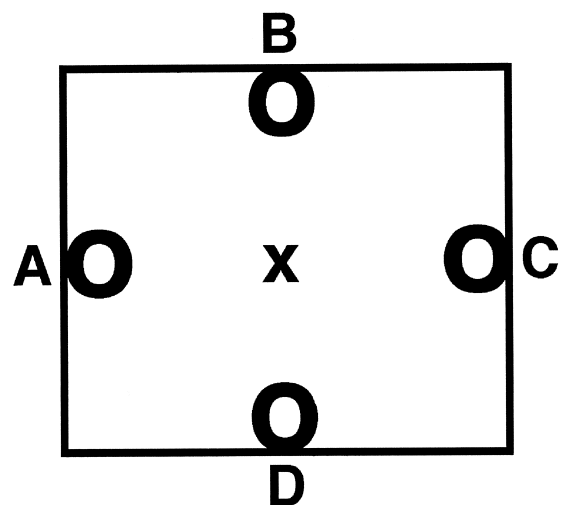

Fig. 1: Diagrammatic representation showing a dorsal view of the floor of the arena used to test for spatial learning in *Oxyopes salticus*. Dimensions of the arena: 25 cm wide, 22 cm deep. Four holes (A, B, C and D), 4-cm in diam., were cut into the arena floor as shown. The spider was placed in the centre of the arena (X) and facing hole B at the start of each trial. See text for details.

this position, the lamp provided a source of bright light and heat resulting in a temperature near the floor of the arena that ranged between 35–36°C. Preliminary experiments had shown that these spiders will move to a darkened chamber to avoid these brightness and temperature conditions, if presented either alone or in combination with one another (unpubl. data).

The experimental procedure used was modified from that described by Holtzman (1998) for his work on snakes. To summarise, in order to acclimate the spiders to the apparatus (pre-testing trials), each animal was removed from its glass container and placed in a small glass vial (2 cm diam., 5 cm high) with an open top. The open end of the vial was placed in the centre of the arena (Fig. 1, X) and then removed when the spider had positioned itself on the arena floor with its head facing hole B. All of the floor holes were open and each led to an L-shaped plastic tube running beneath the arena floor, which allowed the spiders to escape the aversive conditions of light and heat. The L-shaped tubes provided constant darkness and an air temperature of 23 ± 1°C. When placed inside the chamber, each spider moved rapidly, exploring the interior of the arena, and crawled down the first hole encountered. It was allowed to remain in the L-shaped tube for 4 min and then placed back into the centre of the arena (one pre-testing trial). Each spider received five pre-testing trials/day over a 3-day period. As a result of the pre-testing trials, each spider had entered each of the four holes at least three times. A chi-squared analysis (Sokal & Rohlf, 1995) showed that the spiders did not exhibit any preference (position or turning bias) for a particular hole ($\chi^2 = 1.32$, $p > 0.5$). To avoid any possible effects of odour cues or silk deposits on subsequent trials, the arena floor and L-shaped tubes were thoroughly cleaned with a damp, soaped sponge after each trial.

Spatial learning trials began 24 hr after the last day of pre-testing. During these trials, only one of the four holes in the floor of the arena remained open, leading to an L-shaped escape tube (correct escape response). The remaining three holes were covered at their entrances by square pieces of black Plexiglass©. Twenty spiders were randomly assigned to each of four test groups: (a) group 1 (hole A open); (b) group 2 (hole B open); (c) group 3 (hole C open); (d) group 4 (hole D open). At the beginning of a trial an individual spider was introduced onto the centre of the arena floor as described above and allowed to explore the arena floor until the open hole (escape route) was found. The spider was allowed to remain in the L-shaped tube for 4 min and then placed in the glass vial for 1 min before the next trial (5-min intertrial interval). Each spider received 10 trials per day over a five-day period. The arena and L-shaped tubes were cleaned after each trial as previously described.

For each trial, we recorded the number of incorrect responses, the amount of time (min) required by each spider to find the open hole (correct response), and the route (pathway) taken by the spider in its exploratory movements. A response was considered incorrect if the spider made contact with its pedipalps and/or front legs with any of the closed holes. All observations were made
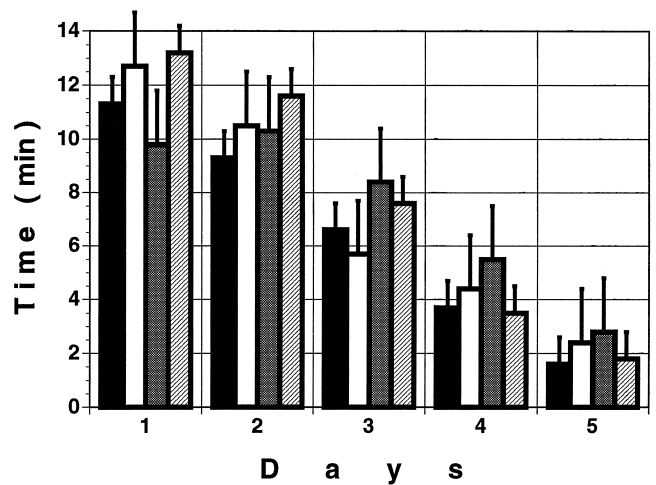

Fig. 2: The amount of time (min) required by individuals of *Oxyopes salticus* to locate the correct opening leading to an escape route over a 5-day testing period. Data expressed as means; vertical lines represent SD. From left to right: test group 1 (black bars), group 2 (unshaded bars), group 3 (stippled bars), and group 4 (hatched bars).

in a darkened room behind a one-way mirror to minimise any effect of the observer on the spider, and all trials were filmed using a Sony MVC-G3 video camera. The arena was placed on a wooden table whose legs were elevated on styrifoam platforms to reduce ground vibrations. All statistical procedures followed those described by Sokal & Rohlf (1995).

We conducted extinction trials to determine whether access to an open hole reinforces spatial learning. Extinction trials were conducted on 20 spiders (five spiders randomly chosen from each test group) that had previously demonstrated spatial learning in the arena. Six hr after the last test trial on day 5, each of these spiders was placed individually in the arena with all of the escape holes blocked with Plexiglass©. Each spider was subjected to 10 extinction trials/day for 5 days as described previously. The amount of time (min) required
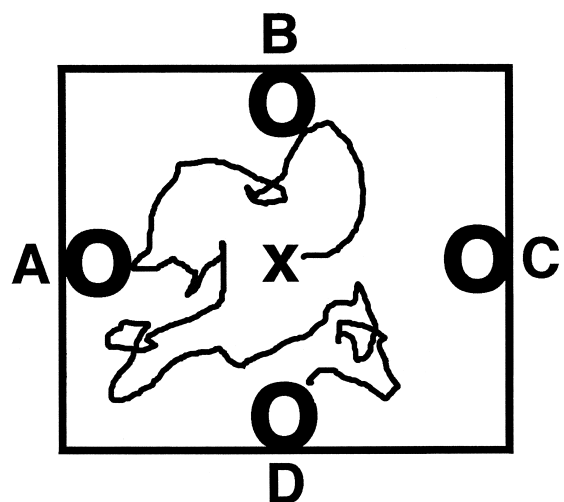

Fig. 3: Actual route taken by an individual spider (*Oxyopes salticus*) from group 4 on the third trial of day 1. The spider was placed at the centre of the arena (X) and facing hole B at the beginning of each trial. See text for details.

by each spider to attempt to enter the hole that had previously been open for that group was recorded.

Results

The results indicate that *O. salticus* has the ability to learn the location of an escape route. The amount of time required for the spiders from all test groups (G1–G4) to locate the open hole allowing them to escape from the aversive stimuli decreased significantly over the 5-day testing period (Fig. 2). An analysis of variance (ANOVA, randomised block design; Sokal & Rohlf, 1995) showed a significant effect for days of testing on running time ($F=178.7$, $p<0.0001$), and no significant difference between test groups for each day of testing ($p>0.50$). A Scheffe F-test showed that the amount of time required to locate an open hole decreased significantly between day 3 and day 4 ($F=46.7$, $p<0.01$).

This decrease in running time as a function of experience is also reflected in the actual pathways taken by individual spiders from their initial starting points in the arena to the correct escape hole. For example, Fig. 3 shows the pathway taken by an individual spider from group 4 on its third trial of day 1, and this is typical for the spiders from all test groups on day 1. At the beginning of these initial trials, the spiders would typically run rapidly around the floor of the arena in a random fashion as shown in Fig. 3. This spider made contact with hole B (closed), then made a looping pattern before contacting hole A (closed), and finally, after a series of random movements made contact with hole D (>10 min), leading to the escape tube. By the third trial on day 5, this spider exhibited a faster (<2 min) and more direct route to the escape tube (Fig. 4, D). A similar pattern was observed for all test subjects.

The number of incorrect responses for all test groups also decreased significantly with experience over the 5-day testing period (Fig. 5) ($F=106.3$, $p<0.001$), with no significant groups/days effects ($p>0.50$). The mean number of incorrect responses showed a significant decrease on day 4 (Scheffe $F=27.7$, $p<0.01$).
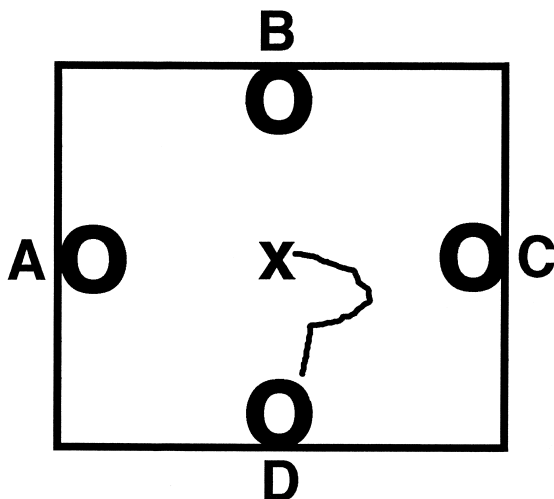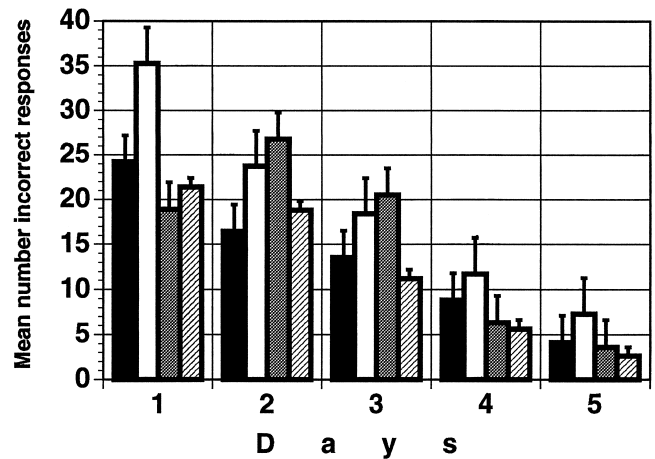
Fig. 5: Number of incorrect responses made by individuals of *Oxyopes salticus* over a 5-day testing period. Data expressed as means of the totals for each spider over 10 trials; vertical lines represent SD. From left to right: group 1 (black bars), group 2 (unshaded bars), group 3 (stippled bars), and group 4 (hatched bars). See text for details.

Spiders exposed to extinction trials showed a progressive increase over the 5-day period in the amount of time required to contact the hole which had previously allowed them to escape the light and heat (Table 1). Their pathways also became progressively more random and by the fourth day they resembled those that they had exhibited on their first day of training.

Discussion

Little previous data exist on spatial learning in spiders. Punzo (2000b) showed that the wolf spider *Trochosa parthenus* (Chamberlin) (Lycosidae) learned a relatively complex maze (six blind alleys) to avoid a mild electric shock. The salticid *Phidippus audax* (Hentz) learned the location of prey in a T-maze and also learned to associate a coloured landmark with the presence of prey (Popson, 1999). Tarsitano & Jackson (1997) showed that araneophagic salticids were able to discriminate between detour routes that did or did not lead to prey. A wandering spider, *Cupiennius salei* (Keyserling) (Ctenidae) used idiothetic orientation and memorised information concerning its previous movements in order to return to a favourable location (Seyfarth *et al.*, 1982). Web-building spiders can learn and remember the position of captured prey within their

Fig. 4: Actual route taken by an individual spider (*Oxyopes salticus*) from group 4 on the third trial of day 5. See text for details.

Day	G1	G2	G3	G4
1	2.1 (0.4)	2.8 (0.6)	3.3 (0.3)	2.3 (0.2)
2	5.7 (1.3)	4.7 (0.9)	8.2 (2.2)	5.9 (1.3)
3	8.1 (2.5)	9.1 (2.9)	11.4 (3.6)	10.7 (2.6)
4	11.7 (3.1)	10.6 (4.2)	9.5 (2.2)	14.6 (5.3)
5	11.4 (1.9)	13.3 (3.7)	12.2 (3.1)	13.9 (3.8)

Table 1: Results of five days of extinction trials for *Oxyopes salticus*. Values represent the time in min required by each spider to attempt to enter the hole which had previously allowed it to escape the aversive conditions inside the arena. Data expressed as means; numbers in parentheses represent ± SD. Spiders were chosen randomly from each test group (G1–G4) ($n=5$/group). See text for details.

webs (LeGuelte, 1969; Lahue, 1973; Sébrier & Krafft, 1993; Foelix, 1996). Female wolf spiders (*Pardosa pallida* Emerton (=*P. distincta* (Blackwall)) whose egg sacs have been removed and placed at another site within an experimental chamber, can learn a more direct route to their location with experience (Peckham & Peckham, 1887). Papi & Tongiorgi (1963) showed that the lycosid *Arctosa variana* C. L. Koch was able to learn novel escape routes under laboratory conditions. Henton & Crawford (1966) showed that the tarantula *Aphonopelma californicum* (Ausserer) (Theraphosidae) was able to exhibit place learning in a simple T-maze.

The present study shows that *O. salticus* is capable of learning a spatial task. Learning is defined as a relatively permanent change in behaviour that occurs as the result of experience (Bitterman, 1975; Davey, 1989). The pathways taken by these spiders in locating an escape route, and the time required to find them, clearly changed with experience. Furthermore, the task employed in these experiments is relevant to their behaviour under natural conditions. The ability to learn where a reliable source of food can be found or the location of suitable shelter sites would certainly contribute to overall fitness (Robinson & Robinson, 1971; Persons, 1999). Salticids, for example, with their highly developed visual capacity, can learn to locate a refuge site more readily with experience (LeGuelte, 1969; Lahue, 1973; Popson, 1999), as well as the route to a potential food source (Seyfarth *et al.*, 1982; Tarsitano & Jackson, 1997). Robinson & Robinson (1971) found that the ogre-faced spider *Deinopis longipes* F.O.P.-Cambridge would position itself above the foraging trails of ants and capture them as they passed by. This study indicates that oxyopids have a similar spatial learning capacity.

The extinction trials showed that *O. salticus* has the ability to locate the correct escape hole without an opening being present. Although this suggests that their ability to find the open hole may not necessarily require any direct cue, actually entering the hole appears to be necessary to reinforce learning. However, the presence of specific topographical or odour cues, which are likely to be present in the natural habitat, have been shown to facilitate spatial learning in vertebrates (Olton, 1978; Janson, 1998; Hughes & Blight, 1999; Punzo, 2000a).

Oxyopids are typically diurnal hunters (Young & Lockley, 1985), although they have also been observed feeding at night (Nyffeler *et al.*, 1987). They are generally considered to be cursorial spiders that have become specialised for a life associated with plants (Nyffeler *et al.*, 1992; Punzo & Kukoyi, 1997), and they regularly move to different locations (patches) where prey are more abundant (Young & Lockley, 1985). Under natural conditions, food is often patchily distributed among locations that can vary spatially and temporally in profitability. The ability to learn spatial cues associated with locations of high prey density, shelter sites, and/or escape routes, would decrease searching behaviour and increase the foraging efficiency of this spider.

Animals are capable of perceiving and responding to visual or chemical cues in their environments to varying degrees, depending on the sensitivity of their receptor organs (Blest, 1987; Morse, 1993; Persons & Uetz, 1996; Popson, 1999). Those which inhabit topographically/chemically rich habitats might rely more heavily on spatial cues (Gendron & Reichman, 1995; Healy & Hurly, 1995; Persons, 1999). *Oxyopes salticus* typically inhabits areas with high plant densities characterised by high vertical stratification. It is not surprising, therefore, that this spider can utilise spatial learning to find shelter sites. Future studies should investigate whether or not *O. salticus* utilises spatial learning in other ways, such as remembering specific locations where previous foraging success was high. It would also be valuable to determine to what extent, and in what context, *O. salticus* utilises other types of learning (i.e. habituation, operant and classical conditioning, avoidance learning) to solve various kinds of tasks.

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