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The effects of early experience on open field behaviour in the lynx spider *Oxyopes salticus* Hentz (Araneae, Oxyopidae)

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Summary

Studies were conducted to test the effects of rearing conditions (environmental complexity) on the locomotor activity and exploratory behaviour of field-collected (FC) and laboratory-reared (LR) adult females of the lynx spider *Oxyopes salticus*. Spiders were assigned randomly to small or large cages that either were empty (impoverished condition, IC) or contained vegetation, rocks, leaf litter, and cardboard cylinders (enriched condition, EC). We tested the following behaviours in a square, open-field arena consisting of 36 quadrats divided into a central, an intermediate, and an edge (outermost) sector: (1) the number of times each subject moved from one quadrat to another; (2) the time spent by each spider in each sector of the arena; and (3) the total number of quadrats entered by each spider during a 30-min test period (a measure of exploratory behaviour). LR spiders spent significantly more time in the edge sector, whereas FC spiders spent more time in the central and intermediate sectors. Differences between LR and FC animals were most pronounced under EC conditions. LR spiders were less active than FC animals, and IC spiders were less active than those reared under EC conditions. EC spiders from large cages crossed more quadrats than did IC spiders; environmental complexity had no effect on spiders reared in small cages. Also, LR spiders explored fewer of the 36 quadrats than did FC spiders. The implications of these results for researchers conducting studies on arthropods and making comparisons between the behaviour of captive-bred animals and their counterparts in the field are discussed.

Introduction

Although it has been demonstrated that environmental factors such as ambient temperature and moisture can influence many morphological, physiological, and developmental processes in ectotherms that may have profound effects on phenotypic traits later in life (May, 1985; Burger, 1991; Punzo, 2000), there is little information available on the effects of early experience and/or the complexity of environmental rearing conditions (enriched vs. impoverished conditions) on subsequent behaviour in invertebrates, including arthropods (Punzo, 1996). In fact, as recently as 1985, it was argued that the development of invertebrate central nervous systems (CNS) was so rigidly programmed as to render them qualitatively different from those of vertebrates (Easter *et al*., 1985), which were considered to exhibit a higher degree of plasticity and have patterns of neural connections which were more directly responsive to early experiential conditions (Punzo, 1985; Nilsson *et al*., 1999).

A number of studies on arthropods have helped to change this view, showing that CNS neurons may exhibit prolonged periods of malleability and that environmental complexity can influence the number of cells, synaptogenesis, and the degree of dendritic proliferation. For example, significant changes in the number and spinal morphology of neurons (Keynon cells) in the mushroom bodies of brains of newly emerged honeybee workers (*Apis mellifera*) occurred after their first orientation flight from the nest (Coss & Brandon, 1982). Lomassese *et al*. (2000) reared some groups of crickets (*Acheta domesticus*) in cages that provided them with food, water, hiding places, branches, different types of surfaces, and allowed them to interact with conspecifics, hear the calls of conspecific males, and smell various plant fragrances (enriched conditions, EC). Others were reared in isolation, in cages devoid of objects, and kept in constant darkness (impoverished conditions, IC). They found that the mushroom bodies of EC crickets contained more neurons that IC crickets. Sandeman & Sandeman (2000) found that the rate of proliferation of interneurons in the olfactory lobes of crayfish (*Cherax destructor*) was also sensitive to early rearing conditions. A study by Carducci & Jakob (2000) showed that salticid spiders (*Phidippus audax* (Hentz)) reared in larger cages containing painted wooden dowels (increased environmental complexity) exhibited a higher degree of exploratory activity in an open field area.

There is also a growing body of evidence that a wide variety of animals including mammals (Höhn *et al*., 2000; Stoinski *et al*., 2000), birds (Heezik & Seddon, 1998), and reptiles (Burghardt *et al*., 1996) collected from the field often exhibit improved performance at certain tasks as compared with that exhibited by captive-reared conspecifics. This suggests that field-caught animals may be exposed to more environmentally complex conditions (McPhee *et al*., 1998). There is virtually no information on differences between field-collected and laboratory-reared arthropods. In the only study to date, field-collected jumping spiders (*Phidippus audax*) exhibited enhanced activity and exploratory behaviour as compared with conspecifics reared in captivity (Carducci & Jakob, 2000).

The purpose of this study was to examine the effects of rearing conditions (environmental complexity) on the subsequent behaviour of laboratory-reared and field-collected striped lynx spiders (*Oxyopes salticus* Hentz). This spider is typically found in habitats characterised by tall grasses, weeds and shrubs (Punzo & Kukoyi, 1997), and often migrates into crop fields where it is one of the most common predators occurring in agroecosystems (Nyffeler *et al*., 1992). It is an ambush predator that frequently changes patches and feeds on a wide variety of arthropod prey (Punzo, 2001). Open-field tests were used to assess locomotor activity and exploratory behaviour, with the assumption that if these behaviours are influenced by rearing conditions, lynx spiders that had been reared/exposed to more complex (enriched) environmental conditions (EC) should exhibit increased activity and exploration as compared with those exposed to a less complex environment (IC).

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Material and methods

Subjects

Field-collected (FC) adults and juveniles of *O. salticus* were obtained by the use of sweep nets and pitfall traps, as described by Punzo & Kukoyi (1997), from various locations in Hillsborough County, Florida during June and July 1999. They were transported back to the laboratory and maintained separately in plastic cages placed in Precision Model 85 environmental chambers (Boone, Iowa) at 23 ± 1°C, 70% RH, and 14L:10D photoperiod regime. They were provided with water *ad libitum* and fed on a diet of cockroach nymphs (*Periplaneta americana*) and crickets (*Acheta domesticus*).

To obtain laboratory-reared (LR) subjects, egg sacs were collected from field-collected females. The number of spiderlings that emerged ranged from 123–207 per egg sac. Spiderlings were reared individually in 50-ml glass test tubes plugged with cotton until their first moult, and were fed on a diet of fruit flies (*Drosophila melanogaster*) and 1st-instar mealworms (*Tenebrio molitor*). Following the first moult, 100 spiderlings were randomly assigned to each of two sizes of cylindrical cages (small vs. large) and two types of environmental complexity (yielding four possible housing treatments). Large cages were 20 cm high and 25 cm in diameter; small cages measured 10 × 12 cm). The types of environmental complexity were either an EC environment characterised by the presence of leaf litter, small rocks, cardboard cylinders painted with green, red, and yellow vertical stripes, and artificial plants (increased vertical stratification), or an IC environment (empty cage). EC spiders had the opportunity to climb, find shelter, and utilise various perch sites for ambushing prey. Each cage was enclosed in an opaque partition made of black construction paper in order to isolate the occupants visually from those in other cages. Water was provided *ad libitum* by a water dish containing soaked cotton balls located on the floor of the cages. As the spiders grew, larger mealworms and cockroach nymphs (*Periplaneta americana*) were provided twice per week as food items. All cages were housed in a room at 23 ± 1°C with overhead fluorescent lighting (14L:10D).

FC spiders were also randomly assigned to the same treatment groups and maintained under these conditions for 4–5 months before testing, when they reached adulthood. They were maintained on the same feeding schedule and under identical rearing conditions as LR spiders.

Testing procedures

Open-field arenas have been widely used in studies of locomotor activity and exploratory behaviour in a wide variety of animals (Archer, 1973; Poucet *et al*., 1986; Punzo, 1998). In these tests a subject is typically released into an arena where its activity level, the amount of space explored, and/or wall-seeking (stereotactic) behaviour can be analysed.

In these experiments we used an enclosed, square open-field arena (48 × 48 × 10 cm: length, width, height) constructed of Plexiglass. See Carducci & Jakob (2000) for a detailed description and diagrammatic representation of this arena. To summarise, the floor of the arena was marked off into 36 square quadrats, with each quadrat measuring 8 × 8 cm. The central sector of the arena consisted of four quadrats, and was bordered by an intermediate sector consisting of a square of single quadrats (4/side = 12 quadrats). The edge sector (outermost sector, adjacent to the walls) consisted of a square of single quadrats (6/side = 20 quadrats).

Forty-eight FC spiders and 70 LR spiders were each tested once in the open field arena. All spiders tested were females. Females were chosen because of their availability in our sample and also because there is some evidence that females are more mobile than males (Young & Lockley, 1985). Sample sizes were not identical for every test owing to a small percentage of mortality that occurred before testing could take place. Spiders were released individually into the centre of the arena and their locations continuously monitored for one 30-min test period. The floor of the arena was cleaned with a dilute ammonia solution after each trial. All trials were viewed through a one-way mirror to minimise disturbance of the animals and were recorded with a Sony MVC video camera. The following data were recorded for each subject: (1) the number of times each subject moved from one quadrat to another (a measure of overall locomotor activity); (2) the time spent by each subject in each sector of the arena; and (3) the total number of quadrats entered by each subject during the test period (a measure of how much new area was explored). Data were expressed as means ± SE.

Bartlett's test for homogeneity (Woolf, 1968) indicated that the data met the assumptions of parametric statistics. Data were subjected to an analysis of variance (SuperAnova, Abacus Concepts).

Results

A three-factor ANOVA was used to test the three main effects of cage size (small vs. large), origin (field vs. laboratory), and environmental complexity (EC vs. IC) in the open field tests. The time spent by the spiders in each sector of the arena is shown in Table 1. Since these data sets are interdependent, p values were adjusted using a sequential Bonferroni method (Sokal & Rohlf, 1995). LR spiders spent significantly more time in the edge sector than did FC individuals ($F = 66.43$, $p < 0.002$), whereas FC spiders spent more time in the central ($F = 41.27$, $p < 0.002$) and intermediate sectors ($F = 45.73$, $p < 0.002$) as compared with LR individuals. The ANOVA also showed a significant origin/environmental complexity interaction for the central sector ($F = 5.99$, $p < 0.05$), and differences between LR and FC animals with respect to time spent in all sectors were most apparent under EC conditions. No other significant effects of complexity or cage size were observed.

The number of times that spiders moved from one quadrat to another, a measure of overall locomotor activity, was also affected by origin and complexity conditions (Table 2). LR spiders were less active than

Arena sector	Origin	Cage size/Rearing condition			
		Sm/IC	L/IC	Sm/EC	L/EC
Edge	**FC**	870.6 ± 44.7	924.3 ± 61.5	721.4 ± 41.2	752.4 ± 34.1
	LR	984.4 ± 40.2	1129.5 ± 91.1	1142.1 ± 87.6	1227.2 ± 145.4
Intermediate	**FC**	496.4 ± 18.2	573.7 ± 28.5	561.3 ± 24.7	567.6 ± 42.8
	LR	367.2 ± 25.1	350.4 ± 32.6	355.6 ± 36.3	311.2 ± 33.7
Central	**FC**	434.7 ± 33.2	302.7 ± 41.7	519.4 ± 52.3	481.6 ± 29.8
	LR	449.2 ± 28.5	321.4 ± 28.8	302.5 ± 34.4	261.9 ± 19.5

Table 1: The effects of cage size (small, Sm vs. large, L), rearing condition (impoverished, IC vs. enriched, EC), and origin (field-collected, FC vs. laboratory-reared, LR) on the time spent by individuals of *Oxyopes salticus* in each sector of an open-field arena. Data represent time spent in s and are presented as means ± SE. See text for details.

FC animals ($F=7.89$, $p<0.003$) regardless of cage size, and IC spiders were less active than EC spiders ($F=5.33$, $p<0.02$). There was also a significant cage size/complexity interaction ($F=5.03$, $p<0.05$) in that EC spiders from large cages crossed more quadrats than did IC spiders. Environmental complexity had no effect on spiders kept in small cages ($p>0.50$).

With respect to how much new area was explored (Table 2), LR spiders explored fewer of the 36 quadrats than did FC spiders ($F=14.52$, $p<0.001$), regardless of cage size. No other factors were significant.

Discussion

The results of these experiments indicate that environmental complexity (rearing conditions) affected the locomotor activity and exploratory behaviour of female oxyopids. In addition, differences were most pronounced between LR and FC spiders. EC spiders exhibited greater locomotor activity than did their IC counterparts. Furthermore, FC spiders were more active and less likely to spend time near or in contact with the wall of the arena (edge sector). These differences existed in spite of the fact that FC spiders had been kept in captivity for 4–5 months before testing.

These results are in general agreement with those reported by Carducci & Jakobs (2000) for the salticid spider *Phidippus audax*. However, in their study, conditions defining environmental complexity were more artificial and less complex in that a ''rich'' environment consisted of cages provided with a coloured wooden dowel as compared with a ''poor'' environment in which no dowel was placed in the cage. They also showed that the salticids from ''rich'' environments and larger cages oriented toward visually-located prey from greater distances as compared with spiders from ''poor'' environments and smaller cages. The results of the present study on *O. salticus* suggest that environmental complexity, rearing condition, and cage size can affect the behaviour of other spiders as well, and indeed may extend to a variety of arthropods and other invertebrates.

Origin	Cage size/Rearing condition			
	Sm/IC	L/IC	Sm/EC	L/EC
Number of inter-quadrat movements				
FC	16.9 ± 0.24	17.2 ± 0.51	21.1 ± 0.14	23.2 ± 0.44
LR	13.3 ± 0.18	13.8 ± 0.38	17.6 ± 0.22	19.1 ± 0.38
Number of quadrats explored				
FC	16.8 ± 0.38	17.5 ± 1.12	17.7 ± 0.82	18.4 ± 0.41
LR	13.9 ± 1.21	14.1 ± 0.29	13.9 ± 0.29	14.6 ± 0.44

Table 2: Number of times that individuals of *Oxyopes salticus* moved from one quadrat to another in an open-field arena (inter-quadrat movement, a measure of overall locomotor activity), and total number of the 36 quadrats that were explored. FC = field-collected spiders; LR = laboratory-reared spiders; Sm = small cages; L = large cages; IC = impoverished conditions; EC = enriched conditions. Data presented as means ± SE. See text for details.

The results of this study also suggest that the complexity of rearing conditions, cage size, and whether or not subjects are captive-bred or collected in the field, can have profound effects on behaviour, and also force us to question the correlation between data collected on captive-bred animals and data collected from animals under natural (field) conditions. The majority of studies on the effects of cage design, size, and environmental complexity have been conducted on vertebrates, especially mammals, owing to the keen interest that has developed concerning the housing of these animals in captivity and animal welfare issues in general (McPhee *et al*., 1998; Hebert & Bard, 2000; Stoinski *et al*., 2000). The results of this study show that these parameters can affect the subsequent behaviour of arthropods as well. This is especially relevant since many investigators choose to work with arthropods because of their short life spans and the ease with which many of them can be bred in captivity in large numbers.

There are several ways in which environmental complexity may have influenced the behaviour of *O. salticus*. First, the development of the CNS may have been modified in response to EC conditions. It is well known that environmental enrichment can promote increased neurogenesis/synaptogenesis in the brains of birds and mammals. For example, Walsh & Cummins (1979) showed that the diameter of hippocampal neurons was significantly larger in rats reared in groups vs. those that were kept isolated from conspecifics. Trimming the whiskers on one side of the face of rats decreased the responsiveness of neurons in the somatosensory cortex of rats (Diamond *et al*., 1993). Rats reared in groups of 20, in cages provided with novel objects, showed increased neurogenesis in the dentate gyrus of the brain and performed better at spatial memory tasks, than rats reared in isolation in barren cages (Nilsson *et al*., 1999).

Smulders *et al.* (2000) showed that seasonal changes in neuron numbers in the hippocampus of birds are associated with increased foraging activity. Other studies have identified use-induced plasticity in birds and mammals, especially in animals exposed to specific training tasks and/or reared in enriched environments (see review by Rosenzweig & Bennett, 1996). In addition, increased environmental complexity results in enhanced exploratory behaviour in a wide variety of vertebrates (Sahakian *et al.*, 1977; Punzo, 1985; Burghardt *et al.*, 1996; Crabbe *et al.*, 1999; Zimmermann *et al.*, 2001).

Experience has been shown to influence CNS development in insects as well. For example, sensory deprivation decreases the responsiveness of interneurons in the cricket *Acheta domesticus* (Matsumoto & Murphey, 1977). Rapid changes in the dendritic spine morphology of Keynon cells in the mushroom bodies of the honey bee brain were found to accompany their first orientation flight from the hive (Coss & Brandon, 1982). The mushroom bodies of insects are associated with the mediation of numerous complex behaviours including learning, memory, the coordination of complex motor movements, nest construction, stridulation, etc. (see review by Punzo, 1996). The morphology and size of various brain regions of *Drosophila melanogaster* (Heisenberg *et al.*, 1995) and *Acheta domesticus* (Lomassese *et al.*, 2000) are significantly affected by cage size and the degree of interaction with conspecifics (Heisenberg *et al.*, 1995). Changes in the volume of the mushroom bodies in the brains of worker honey bees have been associated with specific tasks and maturation (Withers *et al.*, 1995).

Far less attention has been given to the influence of environmental complexity on CNS development and/or subsequent behaviour in spiders and other arachnids. This study, and that by Carducci & Jakobs (2000) mentioned above, are the only ones that have been conducted on spider behaviour so far. No data are currently available on the effect of rearing conditions/environmental complexity on the morphology of the spider brain. With respect to the relationship between experience and neurochemistry, recent studies have reported that changes in brain monoamine concentrations accompany aggression in the solifugid *Eremobates marathoni* Muma & Brookhart (Punzo, 2002) and the tarantula spider *Aphonopelma hentzi* (Girard) (Punzo & Punzo, 2001). Localisation of brain function in spiders is not as well understood as it is in insects (Punzo, 1988; Foelix, 1996), and the relationships between changes in neurochemistry that accompany experience and brain morphology are not yet known.

Secondly, differences in the behaviour of *O. salticus* may have been caused by increased activity levels in FC spiders, since these animals were more active in the open-field tests than LR spiders. Increased activity may be attributable to nutritional differences between the two groups. Although FC spiders were maintained on a similar diet in the laboratory, they would have been exposed to a much wider variety of prey types before their capture as compared with LR spiders. Perhaps nutritional factors experienced early in life can affect subsequent behaviour and cannot be ameliorated by dietary changes that occur later in the maturational process. It should also be noted that the significant effects of environmental complexity and cage size cannot be attributed to nutritional differences. Increased activity levels could also be the result of differences in respiratory physiology or muscle development between LR and FC spiders, especially if FC spiders are typically more mobile and active under natural conditions, and in larger vs. smaller cages.

Thirdly, FC spiders may have had a greater opportunity to learn and practice behaviours under more heterogeneous field conditions characterised by a higher degree of unpredictability. For example, in the field spiders would be expected to experience a wider array of microhabitats and to encounter a wider variety of other animals, including predators and prey. It has been argued that enhanced learning ability is often associated with environmental heterogeneity (Davey, 1989; Stephens, 1993; Punzo, 1991, 1995, 2000). Encountering a more varied environment may have reduced any tendency toward neophobia and increased subsequent locomotor activities. However, no conclusions concerning the relationship (if any) between learning and differences in behaviour between LR and FC spiders can be reached, since spiders were tested only once.

Fourthly, behavioural differences between FC and LR spiders may be related to subtle differences in selection pressure in one or both populations. Since later-instar juveniles or adults were collected for the FC group, these may represent individuals that had survived selective pressures on earlier life cycle stages occurring in the natural environment. For example, young juvenile spiders in the field that were characterised by reduced mobility, as well as a lower capacity for learning and memory, capturing prey, and escaping predators, may have been selected against, whereas such individuals might have had a higher survival capacity under laboratory conditions.

Finally, the different rearing conditions may have had a negative effect on the development of the visual system. Previous studies have shown that the light regime encountered during development can affect the development of the optic lobe in insects (Barth *et al.*, 1997a) and spiders (Foelix, 1996), as well as mating behaviour in drosophilids (Barth *et al.*, 1997b). Perhaps the lighting conditions in the laboratory impaired the morphogenesis of neural pathways or interfered with neurotransmitters/neuromodulators involved in the transmission of nerve signals from the photoreceptors to the optic lobes.

In summary, rearing conditions have a significant effect on the subsequent behaviour of arthropods as well as vertebrates. Thus, researchers who use arthropods in behavioural research should be aware that captive-bred animals do not necessarily behave in the same way as their counterparts in the field. Any adverse effects of captivity may be offset to some degree by increasing cage sizes as well as the stimulus complexity of the laboratory environment.

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A checklist of the ground-dwelling spiders of coastal dune forests at Richards Bay, South Africa (Arachnida: Araneae)

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Summary

The South African National Survey of Arachnida (SANSA) was initiated to make an inventory of the arachnid fauna of South Africa. Various projects are in progress to prepare inventories of the spider fauna of the different biomes and provinces of South Africa. Between 1996 and 1997 ground-dwelling spiders were sampled with pitfall traps from different stands of coastal dune forest at Richards Bay, KwaZulu-Natal. The forest biome, of which the coastal dune forest forms part, is the smallest floral biome in Southern Africa, covering less than 0.25% of the surface area. This was the first quantitative survey of spiders of coastal dune forest at Richards Bay. Twenty-five families represented by 39 genera and 48 species were recorded. The Lycosidae was the most abundant family (589 individuals), representing 71% of all the spiders sampled, followed by the Ctenidae (102) with 12% and the Thomisidae (23) with 3%. The most abundant spider species was an undescribed lycosid species, followed by *Ctenus gulosus* Arts, 1912 (Ctenidae). The Lycosidae was the most species rich family (7) followed by the Corinnidae (6), while 13 families were represented by single species. Forty-eight species were new distribution records for the Richards Bay area.

Introduction

Conservation biologists have started to recognise the importance of the invertebrate component in the functioning of healthy ecosystems. However, meaningful conservation cannot take place if the species involved are not known. Although the Araneae constitute an abundant and highly successful group of invertebrate animals, little is still known about their diversity within most ecosystems in South Africa. Compared with areas in the Northern Hemisphere our knowledge of African spiders is particularly sparse and largely restricted to taxonomy, but even here only 16% of the genera have been revised (Dippenaar-Schoeman & Jocqué, 1997). In 1997 the South African National Survey of Arachnida (SANSA) was initiated to make an inventory of the arachnid fauna of South Africa (Dippenaar-Schoeman & Craemer, 2000). As part of SANSA various projects are in progress to prepare inventories of the spider fauna of the different floral biomes and provinces of South Africa.

This pilot study was undertaken to gather information on the species present in different stands of rehabilitated coastal dune forest at Richards Bay in KwaZulu-Natal, South Africa after mining by a local mining company, Richards Bay Minerals (RBM). RBM began the extraction of minerals from coastal sand dunes in 1976. The mining operation required the clearing of 14 km^2 of natural dune forest vegetation, with an obviously devastating effect on the indigenous flora and fauna. Rehabilitation of parts of the mined area began in 1977 and continues to the present day. The rehabilitation process, described in detail by Van Aarde *et al.* (1996a,b), resulted in the formation of a series of stands of regenerating coastal dune forest of known age. Rehabilitation entails the re-shaping of dunes after mining, spreading of topsoil harvested from cleared forest, and the establishment of a fast-growing set of annual and perennial plant species to stabilise the soil. From this point on rehabilitation occurs through a process of natural succession (Mentis & Ellery, 1994), with minimal management input except for removal of exotic invasive plant species.

In this study we record information on spider species present in rehabilitating and unmined coastal dune forest at Richards Bay. Spiders were collected during four trapping periods between 1996 and 1997. Further studies to analyse the effect of season and successional age on the spider communities of both the herbaceous and ground-dwelling spider fauna will be reported on by Wassenaar & Dippenaar-Schoeman (in prep.).

Methods and study area

Spiders were sampled from three mined, rehabilitating stands with median ages of 2, 8 and 16 years. One