

Early Experience Influences both Habitat Choice and Locomotor Performance in Tiger Snakes

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ABSTRACT: Through adaptive developmental plasticity, individuals may function most effectively in the type of environment in which they have spent most of their time. Such habitat-specific modifications may favor active selection of that habitat type later in life, further reinforcing developmentally plastic phenotypic modifications. The interaction between these processes may have profound evolutionary implications. In nature, Australian tiger snakes (*Notechis scutatus*) use a complex mosaic of terrestrial, arboreal, and aquatic habitats. We raised juvenile tiger snakes for the first 11 months of life in enclosures mimicking one of these habitats and then tested their habitat selection when offered a choice of habitat types. Snakes consistently selected the habitat types in which they had been reared, and they were more effective at locomotion in those habitats than in the others. This attachment to a familiar habitat and phenotypically flexible adjustments in order to function effectively in that habitat constitute a positive feedback loop. That is, animals benefit by choosing a familiar habitat because they can fine-tune behaviors in ways that enable them to function better in that habitat, and, by consistently selecting that kind of habitat, they not only reinforce those phenotypically plastic adjustments but also are placed under continuing selection to cope with the challenges (of foraging, predator evasion, etc.) imposed by that habitat type. The end result may be to create ecomorphs, whereby different individuals within a population become specialized for different types of habitats even in the absence of genetic differentiation.

Keywords: imprinting, habitat, plasticity, locomotion, snake.

This article explores the conjunction of two common, widely observed patterns. The first is that of adaptive developmental plasticity, whereby many aspects of an ani-

mal's phenotype (including behavior, physiology, and morphology) are modified by the local environment in ways that facilitate the individual's ability to function effectively within that environment (Stearns 1989, 1992; Schlichting and Pigliucci 1998; Madsen and Shine 2000; Doughty and Reznick 2004; Thorpe and Losos 2004; Yeh and Price 2004). Developmentally plastic responses of this type have been recorded for diverse traits in many species (Werner 1986; Losos et al. 2000; Henry and Harrison 2004; Moore et al. 2006; Downes and Hoefler 2007). The second pattern has attracted less attention but also appears to be very common. It involves developmental plasticity in habitat selection, whereby an individual actively "prefers" to reside in an area that is familiar, or is similar to a familiar area, rather than in any other location (Wecker 1963; Immelmann 1975; Davis and Stamps 2004; Stamps and Davis 2006). Early experience of a specific habitat type or physical location may result in prolonged site tenure throughout the animal's lifetime (Quertermus 1975; Mushinsky 1976; McGuire et al. 1993; Teuschl et al. 1998; Morse 1999) or in philopatry (return after movement or displacement; Papi 1992; Hein and Whitaker 1997; Oliver et al. 1998; Lucas and Baras 2001) and may be mediated by a variety of sensory cues (such as odors [Dittman and Quinn 1996] or geomagnetic [Lohmann et al. 2001] or visual cues [Walcott 2005]). This kind of attachment to a specific place, or kind of place, is very familiar to humans; many people report a longing to return to the familiar places of their childhood. Cases of natal philopatry in nonhuman species (e.g., fish, turtles, lizards, mammals, birds, amphibians, insects, and spiders; Mushinsky 1976; McGuire et al. 1993; Weatherhead and Forbes 1994; Dittman and Quinn 1996; de Fraipont et al. 2000; Johannesen and Lubin 2001; Sumana et al. 2005; Lee et al. 2007) suggest an analogous attachment to a familiar type of location in other taxa.

Although both of these phenomena are widely recognized, the consequences of their interaction have attracted little attention (Davis and Stamps 2004). Nonetheless, the combination of developmental plasticity in both phenotypic traits and early habitat experience may have important evolutionary consequences. Because

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adaptive plasticity will fine-tune attributes of an organism for a specific environment, active selection of that type of environment not only will reinforce the fitness effects of any such fine-tuning but also will expose the organism to selective regimes (e.g., on optimal foraging modes, predator avoidance) specific to that habitat. In turn, additional fine-tuning of phenotypic traits will enhance the adaptive value of early habitat experience. The end result is a positive feedback loop where organisms are under intense selection to specialize on specific habitat types, becoming better and better at functioning within such sites and more and more determined to return to such sites if displaced.

Although these ideas are simple, they appear not to have been tested. As a first step, the process is straightforward. We need a species that typically exploits a mosaic of habitat types, each of which requires slightly different behaviors, physiologies, or morphologies for optimal performance. Presumably, in many cases a single individual exploits each of the available habitats, but often there must be substantial variation through space and time (and thus, variation among individuals) in the relative frequency of use of each of those alternatives. Our hypothesis predicts that if we raise young individuals in just one of those habitat types, two different kinds of developmental plasticity will manifest themselves. First, the individuals will perform better in the environment in which they have been raised. Second, if given a choice of a habitat mosaic, individuals will actively select the kind of habitat with which they are familiar. We experimentally manipulated the rearing conditions of young snakes to test these two predictions.

Methods

Study Species

The Australian tiger snake *Notechis scutatus* is a highly venomous elapid species that is widely distributed throughout southern and eastern Australia (Cogger 1992). Although typically found in swampy areas where frogs (their main prey items) abound, tiger snakes occur in a variety of habitats throughout their range and have been particularly successful on many offshore islands (Keogh et al. 2005). Although tiger snakes usually forage in terrestrial habitats, arboreality and aquatic foraging are common also (Webb 1981; Schwaner 1985; Mirtschin and Davis 1992). On offshore islands, tiger snakes often bask on top of small shrubs or fences (Worrell 1958; Rawlinson 1974; F. Aubret, personal observations). Tiger snakes also have been reported to climb large trees and to take nestling birds from tree cavities (Webb 1981; Shine 1987). Tiger snakes also forage underwater for tadpoles and fishes, the main prey types for some snake populations (Mirtschin and Davis

1992). Tiger snakes thus fulfill the requirements for our study in that they exploit a mosaic of habitat types (trees, land, water) that impose different locomotor challenges (climbing vs. crawling vs. swimming)

Experimental Procedure

The study animals were neonates born to five pregnant female snakes captured in Herdsman Lake (HL; 31°55'44"S; 115°48'19"E; two litters), a nature reserve near the city of Perth, Western Australia, and Williams Island (WI; 35°01'54"S; 135°58'28"E; three litters) on the southern tip of Eyre Peninsula, South Australia. This island population has been separated from their mainland ancestors for <10,000 years, with minimal genetic divergence (Scott et al. 2001; Keogh et al. 2005). Neonates were measured <24 h after parturition. Body mass was quantified with a digital scale (± 0.01 g); body length and snout-vent length were measured to the nearest 5 mm. Neonates were individually housed in plastic boxes (15 cm \times 10 cm \times 5 cm), with a water dish and shelter and paper towel as substratum. All snakes were fed dead baby mice once a week. When the snakes were 1 month old, we randomly selected a few neonates per litter and allocated 11–13 animals to each of three treatments: terrestrial, aquatic, and arboreal rearing conditions. Similar numbers of neonates from each litter were allocated to each treatment group to balance potential maternal (litter-of-origin) effects. The animals were then raised under the following conditions for 11 months:

Aquatic environment. The 13 neonates (five WI and eight HL) were housed in four plastic boxes (80 cm \times 50 cm \times 25 cm) filled with 15-cm-deep water. A basking platform under a lamp on one corner of each enclosure provided heat for 12 h each day. Each enclosure contained a shelter (upside-down flower pot with several holes to allow snakes to come and go) on a floating (polystyrene) island measuring 15 cm \times 15 cm. Ambient room temperature was set at 21°C.

Terrestrial environment. The 11 neonates (four WI and seven HL) were distributed between four enclosures identical to those described above, including the shelter (flower pot) and heat lamp. However, the substratum was gravel-like cat litter (attapulgate), and the only water was in a small dish (too small to allow swimming).

Arboreal environment. Twelve neonates (five WI and seven HL) were distributed among four large compost bins (120 cm tall, 100-cm radius, open at the top). We filled the bins with branches up to 60 cm high and placed the lamp above the bins, warming only the very top of the branches. Thus, snakes had to climb all the way up to access the heat source. Snakes basked on a daily basis, coiled on the top branches. Cat litter was used as sub-

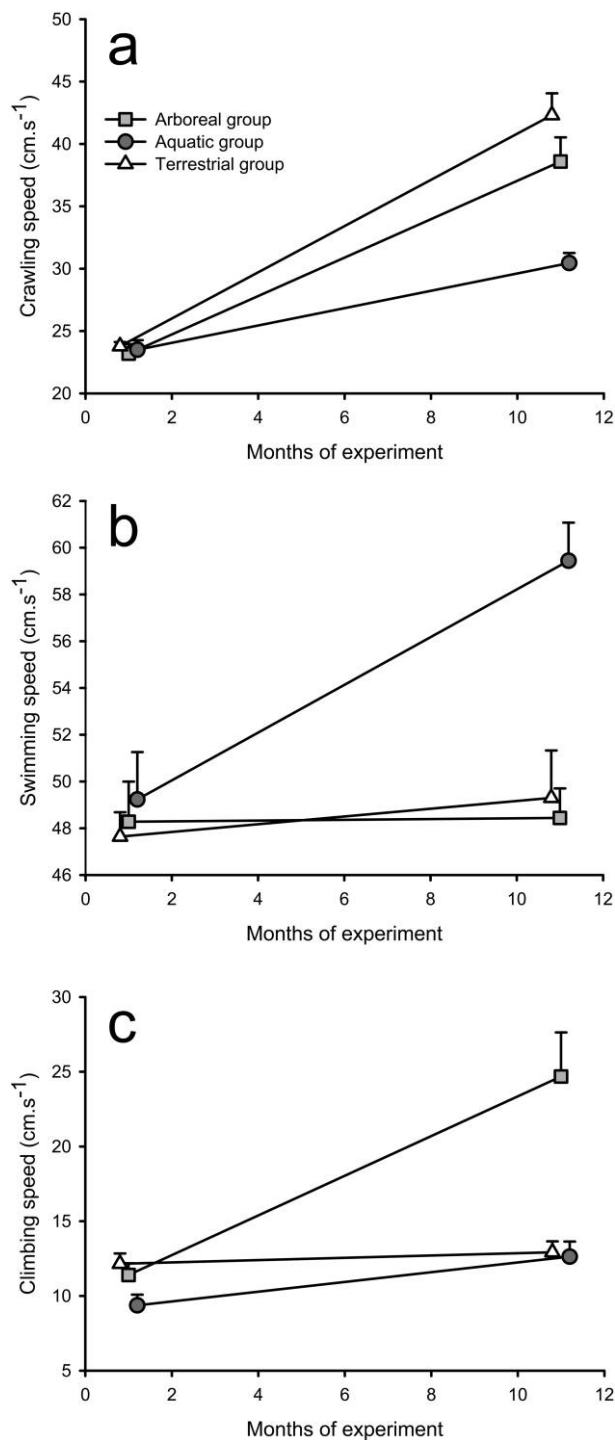


Figure 1: Effects of rearing environment on the young snakes' ability to crawl (a), swim (b), and climb (c). Speeds during terrestrial (a), aquatic (b), and arboreal (c) locomotion were recorded in juvenile snakes that had been raised for 11 months in either a terrestrial, an aquatic, or an arboreal environment (see text for statistical details). The early habitat experience resulted in enhanced locomotor performances. Means + SE are plotted.

stratum, and a water dish (too small to allow swimming) was provided at the bottom of each bin.

All snakes were fed on a weekly basis with small dead mice offered directly to each snake. Snakes were otherwise undisturbed (except for cleaning and watering purposes) and were never handled, in order to minimize stress.

Locomotor Performance

We measured locomotor performance at two stages: just before the snakes were allocated to the treatment groups and after 11 months spent in the respective habitats. To minimize potential effects of familiarity with the testing medium on motivation to escape, we recorded burst (sprint) locomotor performances: snakes were chased along the track to ensure that we measured maximal speeds. Morphological data were recorded concurrently with testing. To compare traits between the two groups, ANOVAs and repeated-measures ANOVAs were applied to log-transformed data. As commonly occurs during captive raising of very young animals, some animals died (four aquatic, two terrestrial, and two arboreal snakes) for unknown reasons. Hence, our sample sizes decreased slightly throughout the course of the experiment. Testing was delayed until the sixth day after the most recent feeding event to ensure that the snakes had fully digested their prey before testing.

We used the performance traits burst swimming speed, burst crawling speed, and climbing speed to quantify different facets of a snake's relative functioning in different habitat types. All trials were videotaped (JVC hard-drive camcorder, 30 GB, 25 frames/s), and recordings were edited on a laptop computer.

Burst swimming speed. To estimate swimming performance, we used a standard procedure adopted in previous studies of snakes (Shine and Shetty 2001; Aubret 2004; Aubret et al. 2007; Aubret and Shine 2008). Snakes were released into the water at one end of a linear swimming track (wooden frame lined with black plastic, recording section 180 cm). Markers painted on the bottom of the pool were used to record swimming speed on 30-cm sections of the track. Maximum speed was maintained by stimulating the snake's tail with an artist's paintbrush. Swimming speed was calculated over 15 sections for each snake, and the fastest performance was retained for analysis.

Burst crawling speed. A similar track was used, but it was filled with cat litter. Neonates were released at one end and were stimulated by gently touching their tails with an artist's paintbrush. Crawling speed was calculated over 10 sections, and the fastest performance was retained for analysis.

Climbing speed. To record climbing speed, we used two

Table 1: Habitat selection in young tiger snakes *Notechis scutatus*

Traits recorded	Arboreal (<i>N</i> = 9)	Aquatic (<i>N</i> = 9)	Terrestrial (<i>N</i> = 9)	<i>F</i> ; <i>df</i>	<i>P</i>
Trial time (h)	11.70 ± .49	11.56 ± .67	11.85 ± .14	.81; 2, 24	.45
Total time in arboreal (h) ^a	6.77 ± 3.25	2.32 ± 2.05	4.19 ± 3.33	5.29; 2, 23	.013
Total time in aquatic (h) ^a	3.15 ± 2.35	8.02 ± 3.46	2.70 ± 2.14	7.13; 2, 23	.004
Total time in terrestrial (h) ^a	1.78 ± 1.59	1.37 ± 2.04	4.81 ± 3.47	5.25; 2, 23	.013
No. times in arboreal ^a	24.44 ± 10.84	23.48 ± 14.54	26.19 ± 11.52	.54; 2, 23	.60
No. times in aquatic ^a	24.44 ± 12.18	27.16 ± 18.69	27.75 ± 15.98	.12; 2, 23	.88
No. times in terrestrial ^a	25.44 ± 12.78	25.12 ± 22.05	31.11 ± 12.69	1.08; 2, 23	.36
No. changes in habitat type ^a	74.33 ± 34.74	76.89 ± 54.33	83.89 ± 39.40	.60; 2, 23	.56
Mean time in arboreal (min)	26.51 ± 33.99	6.31 ± 5.63	12.77 ± 16.49	3.85; 2, 23	.036
Mean time in aquatic (min)	10.02 ± 8.06	19.24 ± 13.29	5.70 ± 2.91	4.13; 2, 23	.029
Mean time in terrestrial (min)	4.24 ± 3.40	2.40 ± 1.41	5.71 ± 3.03	4.13; 2, 23	.029
No. swims ^a	9.11 ± 8.18	30.55 ± 28.71	7.22 ± 8.04	3.26; 2, 24	.056

Note: Behavioral traits of young tiger snakes were recorded when each snake was given a choice between three equal-sized areas, one of which corresponded to the type of habitat (terrestrial, aquatic, or arboreal) in which the young snake had been raised for the preceding 11 months. The table shows mean values ± SDs and results of statistical tests (ANOVA) comparing the three groups of young snakes for each variable.

^a Relative to trial time.

horizontal racetracks separated by a 35-cm gap 1 m above the ground. The gap was filled with horizontally oriented small branches. Snakes were released at one end of the track and were stimulated with the paintbrush as they crawled across the “bridge” of branches to the other side. Any free fall was cushioned in a bucket filled with pine shavings. Climbing speed was recorded on a 30-cm section of the gap.

After completion of each performance test, snakes were returned to their respective environment. Two weeks after all locomotor records were completed, we tested habitat selection as follows.

Habitat Selection

Snakes were individually tested in four large enclosures, each of which incorporated equal areas of all three habitat types. Different shapes and materials were used to recreate each habitat, so that any selection by snakes was based on generic attributes rather than specific scent cues. Each snake was tested once: they were introduced early in the morning in the center of the enclosure and videotaped all day. From the video, we scored the time spent in each area of the enclosure. Room temperature was set to 18°C during the day and 15°C at night, and the lamps were set on an automatic timer (on at 0700 hours, off at 2130 hours). Each treatment group had five HL and four WI snakes, so any potential effects of geographic origin were balanced. Because of nonindependence among proportional scores, we subjected the data to a MANOVA to evaluate overall significance of the treatment effect before conducting individual ANOVAs.

Results

Locomotor Performance

All three treatment groups were similar in body mass, snout-vent length, and body length at the beginning and at the end of the experiment (all $P > .12$). Locomotor performance results were also similar before the habitat manipulation but diverged sharply over the course of the treatments (fig. 1). When tested after 11 months in terrestrial, aquatic, or arboreal enclosures, snakes performed significantly better in their rearing environment than they did when tested in the other habitat types (ANOVAs, all $P < .038$). That is, snakes raised in an arboreal environment climbed 95% faster than aquatic snakes (least significant difference post hoc test; $P < .012$) and 93% faster than terrestrial snakes ($P < .023$). Snakes raised in a terrestrial environment crawled 39% faster than aquatic-raised snakes ($P < .007$) but at a similar speed as arboreal snakes ($P = .33$). Finally, snakes raised in an aquatic environment swam 23% faster than arboreal snakes ($P < .027$) and 21% faster than terrestrial snakes ($P < .032$). Results remained unchanged when speeds were calculated relative to snake body length (all $P < .019$).

Habitat Selection

MANOVA confirmed highly significant behavioral differences among the three groups of young snakes when they were given a choice of three habitat types ($F = 6.93$, $df = 4, 48$, $P < .0002$). Snakes tended to spend most time in the same kind of habitat as the one in which they had been kept for the preceding 11 months (table 1). All snakes

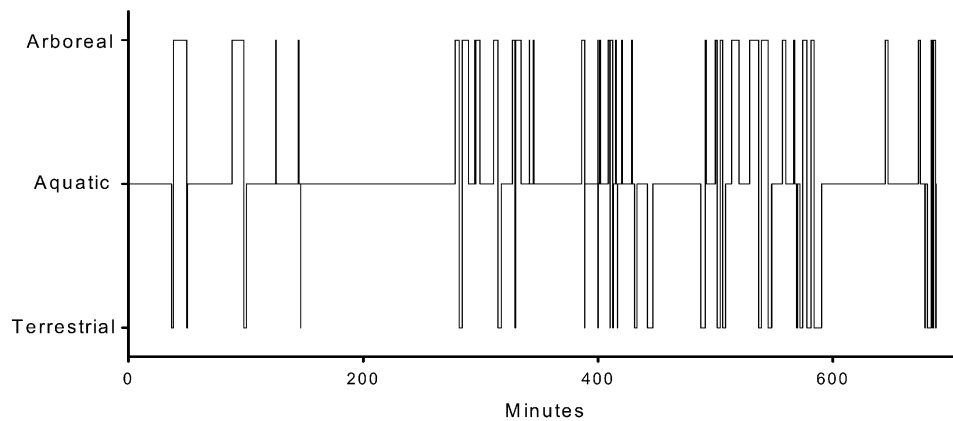


Figure 2: Typical results for habitat selection behavior of a young tiger snake reared in an aquatic environment for 11 months and then released into a large enclosure that offered equal-sized terrestrial, arboreal, and aquatic habitats. This snake visited each habitat a similar number of times (34, 35, and 27 times, respectively), but the average time spent differed significantly among habitats, with most time spent in the aquatic area.

moved extensively (and to approximately the same degree) through all three environments (same number of visits to each habitat type) but stayed longer in the familiar habitat (fig. 2). The aquatic group also entered the water pool more often, but the result fell short of statistical significance.

Discussion

Young tiger snakes raised in three different habitat types exhibited adaptive developmental plasticity in response to rearing conditions, significantly enhancing their abilities in terrestrial, arboreal, or aquatic locomotion. Similarly enhanced locomotor performance as a function of early experience has been reported in lizards (Losos et al. 2000; Downes and Hoefer 2007), snakes (Aubret and Shine 2008), and fish (Olsson et al. 2007). Further, when given a choice, young tiger snakes actively selected habitats similar to their own rearing environment. Radiotelemetry has shown that adult tiger snakes translocated to a new site showed different habitat preferences than did resident snakes (preferring grassy woodlands associated with hills rather than escarpment woodlands and open plains; Butler et al. 2005), possibly reflecting prior experience (Stamps and Swaisgood 2007).

The mechanism or mechanisms underlying such imprinting remain unknown but may involve adaptive behavioral plasticity. By analogy, early exposure to specific food types can influence future prey preference as well as the ability to recognize, capture, and handle food (Burgardt and Hess 1966; Partridge 1976; Krause and Burgardt 2001). Regardless, there is a clear adaptive benefit: the young snakes selected the type of environment in

which their phenotypes had been fine-tuned for optimal functioning. Two mechanistic hypotheses have been proposed to explain this phenomenon (Davis and Stamps 2004): (1) “habitat cuing,” in which prior experience allows dispersers to identify a suitable (optimal) environment, and (2) the “preference-performance hypothesis,” in which higher fitness results from the choice of a habitat of the same type as the natal habitat (Provenza and Balph 1987; Losos et al. 2000; Stamps 2001; Selonen et al. 2007). Our study does not discriminate between these hypotheses, and more work is needed to identify the proximal causations of habitat preference in snakes. Nevertheless, our results suggest an extension of hypothesis 2 in the form of a positive feedback loop: if similar behaviors are exhibited in the wild, then young snakes are likely to be exposed to habitat-specific selective forces that will exaggerate the divergence in abilities revealed by our study. For example, predators might remove the aquatic-raised snakes that are least capable of swimming and the arboreal-raised snakes that are least capable of climbing. The end result will be divergence within the population and matching between habitat preference and performance; individuals that actively select a given habitat also will be the ones that perform best in that habitat type.

Does this phenomenon also affect longer-term evolutionary processes? As noted above, a specific habitat not only may induce change in an individual’s phenotype but may also expose it to different (or novel) selective pressures. This initial step (phenotypic change) may trigger a cascade of consequences because several key characteristics may differ among habitats. For example, resource quality and availability may alter individual behavior (Werner and Anholt 1993; Relyea 2004), and individual behavior may

in turn induce changes in morphology (Webb 1984, 1988; McPeck 1995). Predation pressure and predator type also may induce changes in an individual's behavior and morphology (Woltereck 1909; Brönmark and Miner 1992; Relyea 2004). Hence, adaptive phenotypic plasticity may be a precursor for evolutionary change in facilitating speciation via the classical pathways of allopatric speciation and colonization of novel environments (Pigliucci and Murren 2003; Price et al. 2003; Pigliucci et al. 2006) and perhaps also under sympatric conditions (Chapman et al. 2000; Görür 2000; Adams and Huntingford 2004; de Jong 2005).

In conclusion, our study demonstrates that exposure of a habitat-generalist snake to specific environments early in life can result in correlated modifications in (a) habitat-specific locomotor ability and (b) the cues used for habitat selection. Although our results suggest that natural selection will favor individuals that remain in the natal habitat, future work is needed to document the duration of any such effects. Ideally, we need to translate this experiment to the field and to make direct measurements of the long-term effects (on morphology, physiology, and/or behavior) and putative fitness benefits associated with early habitat experience. Such experienced-based correlations between preference and performance may be relatively common in nature and hence may have important effects on both animal distributions and evolution.

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Left, Williams Island (South Australia) tiger snake; right, Reevesby Island (South Australia) tiger snake out basking.