Functional Ecology 2007
21, 1154–1161

The role of adaptive plasticity in a major evolutionary transition: early aquatic experience affects locomotor performance of terrestrial snakes

F. AUBRET,*† X. BONNET‡ and R. SHINE*

**University of Sydney, Biological Sciences A08, 2006 New South Wales, Australia, ‡Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France*

Summary

1. Many phylogenetic lineages of animals have undergone major habitat transitions, stimulating dramatic phenotypic changes as adaptations to the novel environment. Although most such traits clearly reflect genetic modification, phenotypic plasticity may have been significant in the initial transition between habitat types.

2. Elapid snakes show multiple phylogenetic shifts from terrestrial to aquatic life. We raised young tigersnakes (a terrestrial taxon closely related to sea-snakes) in either a terrestrial or aquatic environment for a 5-month period.

3. The snakes raised in water were able to swim 26% faster, but crawled 36% more slowly, than did their terrestrially-raised siblings. A full stomach impaired locomotor performance, but snakes were less impaired when tested in the environment in which they had been raised.

4. Thus, adaptively plastic responses to local environments may have facilitated aquatic performance (and impaired terrestrial performance) in ancestral snakes as they shifted from terrestrial to aquatic existence.

5. Such plasticity may have influenced the rate or route of this evolutionary transition between habitats, and should be considered when comparing habitat-specific locomotor abilities of present-day aquatic and terrestrial species.

key-words: development, elapid, locomotion, phenotype

Functional Ecology (2007) **21**, 1154–1161
doi: 10.1111/j.1365-2435.2007.01310.x

Introduction

The phenotype of any living organism reflects not only its genotype, but also direct effects of environmental conditions. Some manifestations of environmental effects may be non-adaptive (such as fluctuating asymmetry: Whitlock 1996; Shykoff & Møller 1999). Growing evidence nevertheless demonstrates that natural selection often modifies developmental trajectories in a direction that increases fitness in local environments via enhanced growth, survival and/or reproduction (Bull 1980; Werner 1986; Stearns 1989; Schlichting & Pigliucci 1998; Losos *et al.* 2000; Agrawal 2001). Over recent decades, adaptive phenotypic plasticity has become a central theme in evolutionary biology (Dudley & Schmitt 1996; Pigliucci 2001; Price, Qvarnstrom & Irwin 2003).

Studies of phenotypic plasticity typically have focused on transient effects involving environmental factors that vary over small spatial and temporal scales. Examples include the growth of anti-predator defensive structures in Daphnia and fish in the presence of predators (Woltereck 1909; Bronmark & Miner 1992) and diet-induced developmental polymorphism in caterpillars (Greene 1989). However, phenotypic plasticity also may influence evolutionary transitions at a far grander scale, including major phylogenetic shifts in important traits (Pigliucci & Murren 2003; West-Eberhard 2003). Several recent studies have successfully incorporated adaptive plasticity into macroevolutionary theory (Levin 1988; West-Eberhard 1989; Sultan 1992; Schlichting & Pigliucci 1998; Garland & Kelly 2006).

A key principle linking phenotypic plasticity to macroevolution is the hypothesis that adaptive plasticity may enable, or otherwise facilitate, major evolutionary transitions (see Crews 1994; Leclaire & Brandle 1994; Wimberger 1994; Shine 1995; Gravilets, Li & Vose 1998). For example, it has been proposed that phenotypically plastic responses of reptilian embryos to incubation temperature facilitated the evolutionary transition

---

†Author to whom correspondence should be addressed. E-mail: faubret@mail.usyd.edu.au

from oviparity (egg-laying) to viviparity (live-bearing) in more than 100 separate phylogenetic lineages of lizards and snakes (Shine 1985, 2004). In some but not all reptile species, higher incubation temperatures enhance offspring viability (Shine 1999); and viviparity arose within many of these groups as a way of exposing the eggs to higher temperatures via the female's ability to adjust its body temperature over ambient temperature variations. Maternally retained embryos were thereby kept warmer and developed into more viable offspring (Mell 1929; Sergeev 1940; Shine 1983, 1985, 2004). Overall, adaptive phenotypic plasticity may augment an individual's ability to occupy a new habitat (Baldwin 1896; Holway & Suarez 1999; Price *et al.* 2003; Yeh & Price 2004), exposing founding populations to novel selection pressures and therefore creating the opportunity for genetic assimilation (Waddington 1942, 1961; Pigliucci, Murran & Schlichting 2006).

The hypothesis that adaptive phenotypic plasticity facilitates major evolutionary transitions requires that the founding population exhibits either a pre-adapted phenotypically plastic feature that enables the population to explore a novel habitat, or a feature that acquires phenotypic plasticity in response to exposure to the novel habitat. Although we cannot directly measure phenotypic plasticity in any founding population of an ancient radiation, we can assess the presence of the appropriate phenotypic plasticity in present-day species. The critical taxon in this respect is the outgroup of a clade that has passed through a major evolutionary transition. If the outgroup species retains the ancestral habitat, it may well retain the ancestral state for phenotypic plasticity also. We focus on four groups of aquatic snakes, each of which has independently arisen from a terrestrial ancestor within the Elapidae (front-fanged snakes) (Keogh 1998; Heatwole 1999). These groups are the hydrophiid sea-snakes, the laticaudid sea-snakes, the water cobra *Boulengerina annulata*, and the aquatic coral snake *Micrurus surinamensis* (e.g. Heatwole 1999).

The hydrophiid sea-snakes are especially interesting. The 57 members of this group arose relatively recently from a small clade of terrestrial, viviparous Australian snakes, the 'Notechis group' (Keogh 1998). Of the 20 genera of Australian elapids, *Notechis* itself is most widely distributed, and occurs on many oceanic islands and coastal swamps (Cogger 1992). This situation may well resemble that in which the initial evolutionary transition to aquatic habitats occurred; indeed, Australian tigersnakes (*Notechis scutatus*) often forage in the water (e.g. *N. scutatus kreftii*: Mirtschin & Davis 1992). Moreover, tigersnakes show significant phenotypic plasticity in many traits (Aubret 2004; Aubret, Shine & Bonnet 2004a; Bonnet *et al.* 2004).

We use the tigersnake as a model for the ancestral phenotype of hydrophiid sea-snakes, at least with respect to major habitat (terrestrial *vs* aquatic). We tested if this model for the ancestral phenotype has pre-adapted phenotypic plasticity that augments the ability to occupy the new environment and, therefore, could facilitate a transition from the terrestrial to aquatic habitat. We have done so by measuring plasticity in locomotor performance of young tigersnakes by manipulating the habitat in which the snakes were reared (terrestrial *vs* aquatic).

Materials and methods

STUDY SPECIES

The Australian tigersnake, *N. scutatus*, is a highly venomous elapid species that is widely distributed throughout southern and eastern Australia (Cogger 1992). Mean adult body lengths vary geographically, but generally average 1–2 m (Shine 1987; Schwaner & Sarre 1988). Tigersnakes forage both on land and underwater, taking a diverse range of prey ranging from frogs to nestling birds (Shine 1987; Aubret *et al.* 2004b). Some populations forage mostly on aquatic prey (tadpoles, fishes: Mirtschin & Davis 1992) whereas others live in areas without permanent freshwater bodies and thus, depend entirely upon terrestrial foraging (Bonnet *et al.* 1999, 2002; Aubret *et al.* 2004b). A previous comparison between two populations of tigersnakes from western Australia suggested that plasticity may play a role in matching locomotor performance to local conditions (Aubret 2004). Neonatal snakes from a swamp-dwelling mainland population were similar to neonates from a more arid island population in terms of swimming speed, stamina, apnoea capacities (time spent underwater before surfacing to breathe) and swimming behaviour. However, adult mainland snakes had greater apnoea capacities and faster burst swimming speed than did island snakes. Mainland adult snakes also spontaneously swam underwater for a longer period of time, and a higher proportion filled their lungs whilst surface swimming compared with island specimens (Aubret 2004). These results suggest that early experience may have long-term measurable effects on swimming performance in a wild population of snakes.

EXPERIMENTAL PROCEDURE

The study animals were neonates, born to 10 pregnant female snakes captured in Herdsman Lake (S31 55′44″; E 115 48′19″), a nature reserve near the city of Perth, Western Australia. This perennial lake contains abundant frogs, and these constitute the major dietary items for local tigersnakes (Aubret *et al.* 2004b). At this site, tigersnakes are found both in aquatic and terrestrial habits (Aubret 2004). Neonates were measured < 24 h after parturition. Body mass (BM) was quantified with a digital scale (± 0·01 g); body length (BL) and snout-vent length (SVL) were measured to the nearest 5 mm. Neonates were individually housed in plastic boxes (15 × 10 × 5 cm), with a water dish, shelter and paper towel as substratum. All snakes were fed dead baby mice once a week. When the snakes were 2 months old, we randomly selected two neonates per litter, and allocated these 20 animals to one of two treatments: terrestrial *vs* aquatic rearing conditions. The animals were raised under these conditions for 5 months.

Aquatic environment

The 10 neonates (six males and four females) were housed in two plastic boxes (50 × 50 × 40 cm) filled with 10 cm deep water. A basking rock was available on one side of each enclosure. A shelter (a rock covered by a flower pot) was provided on the other (colder) side of the enclosure, and could be accessed only by diving underwater, through a hole in the side of the flower pot. All young snakes were observed swimming, diving and moving between the shelter and the basking rock on regular basis.

Terrestrial environment

The 10 neonates (six males and four females) were distributed between two enclosures identical to those described above, but with a mixture of sand and sawdust as substratum and a small water dish (too small to allow swimming). All young snakes were frequently observed basking on the rock before returning to the shelter.

In both treatment groups, heating was provided (three periods of 15 min per day) by a Na+ high pressure lamp (600 W), directed towards the basking rock. The young snakes basked every day, and to do so they had to crawl or swim from the shelter to the other side of the cage. The room temperature was maintained at 15 °C by night and 27 °C by day (including in testing periods). The mean selected body temperature of tigersnakes in captivity is close to 27 °C (Ladyman & Bradshaw 2003).

LOCOMOTOR PERFORMANCE RECORDS

We focused on locomotor performance as a fitness-relevant measure of the animal's ability to function both in the ancestral habitat (land) and the novel habitat (water). Locomotor traits were measured twice for each snake: at the beginning of the experiment and after 5 months spent in the respective habitats (i.e. at 2 months and 8 months of age). Morphological data were recorded concurrently with testing, at the start and at the end of the experiment. To compare traits between the two groups, ANOVAs were applied to log-transformed data. As commonly occurs during captive raising of very young animals, some died (three 'aquatic' and two 'terrestrial' snakes) for unknown reasons. Hence, our sample sizes decreased slightly throughout the course of the experiment and degrees of freedom in the statistical analysis vary among tests. Excluding the 'full stomach trials' (see below), testing was always delayed until the sixth day after the most recent feeding event to ensure that the snakes had fully digested their prey prior to testing. We selected the following performance traits to quantify different facets of a snake's relative functioning in aquatic *vs* terrestrial habitats.

BURST SWIMMING SPEED

To estimate swimming performances we used a standard procedure adopted in previous studies (Shine & Shetty 2001; Shine *et al.* 2003; Aubret 2004; Aubret *et al.* 2004c). Snakes were released into the water at one end of a linear swimming track (glass aquarium; recording section of 170 cm). Using a digital stopwatch (precision 0·1 s), we recorded the time taken for the snake to reach the other end of the pool. Maximum speed was maintained by stimulating the snake's tail with an artist's paintbrush. This test was done twice in succession and the fastest performance retained for analysis.

BURST CRAWLING SPEED

Neonates were released at one end of a 100 cm terrestrial raceway with sawdust as the substratum. As above, the snakes were stimulated to keep moving by gently touching their tails with an artist's paintbrush.

NON-FORCED SWIMMING TRIALS

Snakes were dropped from 5 cm above the water level into a circular track (average diameter 94 cm) containing 15 cm deep water. Immediately upon release, every animal began to swim around the track; they were not touched or disturbed for the next 60 s. Over this period, we recorded the number of laps completed, and the time spent swimming *vs* resting (percentage of activity).

APNOEA SCORES

We used an opaque PVC tube 10 cm in length and 2·5 cm in diameter, closed at one end. The diameter of the tube was large enough to allow easy movement of the snake inside it. Snakes were removed from their cage, and the open end of the tube was presented to them. As soon as the snake voluntarily entered the tube, the unit was fully immersed in a pool of water. We recorded the time that the snake remained underwater before surfacing to breathe as the *free apnoea score*. The following day, the test was repeated except that this time, we attempted to mimic a predator by moving above the water and touching the snake underwater with a stick each time it was about to reach the surface. This stimulus encouraged the animal to prolong the duration of its time underwater, presumably until its need to breathe overcame the perceived risk of predation. The time taken to surface was recorded as the *forced apnoea score*.

Table 1. Body size and locomotor performances in juvenile tigersnakes at the beginning and end of the experiment

	Aquatic (N = 7)		Terrestrial (N = 8)	
Traits recorded	2-months-old	7-months-old	2-months-old	7-months-old
Body mass (g)	7·29 ± 0·48	13·95 ± 0·93	7·18 ± 0·41	14·40 ± 1·14
Snout vent length (cm)	20·50 ± 0·47	24·69 ± 0·65	20·20 ± 0·55	25·55 ± 0·64
Body length (cm)	23·97 ± 0·54	28·93 ± 0·85	23·98 ± 0·74	29·85 ± 0·75
Body condition	7·18 ± 0·48	14·53 ± 0·93	7·29 ± 0·51	13·82 ± 1·14
Burst crawling speed (cm/s)	9·83 ± 0·50	14·26 ± 1·54	9·28 ± 0·84	19·47 ± 0·89
Burst crawling speed (BL/s)	0·46 ± 0·03	0·49 ± 0·05	0·43 ± 0·04	0·64 ± 0·03
Free apnoea score (s)	173·10 ± 30·53	389·68 ± 58·78	228·66 ± 22·54	381·05 ± 100·00
Forced apnoea score (s)	339·32 ± 45·76	659·72 ± 58·31	418·78 ± 83·62	301·13 ± 54·68
Burst swimming speed (cm/s)	33·68 ± 5·62	34·71 ± 0·71	31·23 ± 1·97	28·67 ± 0·87
Burst swimming speed (BL/s)	1·39 ± 0·20	1·20 ± 0·03	1·29 ± 0·05	0·95 ± 0·02
Circular track				
Distance swum (cm)	333·70 ± 47·48	224·93 ± 40·66	338·40 ± 80·80	135·13 ± 15·22
Distance swum (BL)	13·78 ± 1·77	7·90 ± 1·53	14·10 ± 3·01	4·43 ± 6·48
Activity time (%)	86·67 ± 4·20	54·99 ± 9·18	88·80 ± 4·65	54·55 ± 6·67
Average swimming speed (cm/s)	6·28 ± 0·79	7·93 ± 1·39	6·40 ± 0·57	4·48 ± 0·65
Average swimming speed (BL/s)	0·26 ± 0·03	0·28 ± 0·05	0·27 ± 0·02	0·15 ± 0·02

BL, body length. Mean values ± SE are given.

EFFECT OF A FULL STOMACH ON LOCOMOTOR PERFORMANCE

After completion of the last series of tests (i.e. after 5 months' exposure to either aquatic or terrestrial life), snakes were fed as usual and then tested the following day for burst crawling speed. The next day, forced apnoea scores were recorded also. A week later, snakes were fed and their burst swimming speed was recorded the following day.

Results

Neonates from the two treatment groups did not differ significantly in initial body size (body mass, snout vent length, body length or body condition; all $P > 0·47$) or locomotor performance (burst crawling, burst swimming and apnoea performances, nor in any of the variables recorded along the circular swimming track; ANOVAS; all $P > 0·10$ – see Table 1). Within each treatment group, there was no significant difference in any of the performance records between males and females at the start of the experiment (All $P > 0·17$), nor at the end (All $P > 0·10$); thus males and females were pooled for analysis. Below, we describe the changes over time of each trait from the beginning to the end of the experiment (Table 1).

FEEDING RATES AND BODY SIZES

The two treatment groups were fed similar amounts of food throughout the experiment (on average 0·07 g ± 0·01 g of food per day; Repeated measure ANOVA; Wilks' $\lambda = 0·75$, $P = 0·22$; effect of treatment $F_{1,17} = 0·37$; $P = 0·55$). Consequently, both treatment groups grew at similar rates and thus exhibited similar mean body mass ($F_{1,16} = 0·05$; $P = 0·82$), total length ($F_{1,16} = 0·67$; $P = 0·42$), snout vent length ($F_{1,16} = 0·90$; $P = 0·36$), and body condition (body mass relative to snout vent length – $F_{1,15} = 0·56$; $P = 0·46$) at the end of the experiment.

BURST SWIMMING SPEEDS

When re-tested after 5 months, the snakes raised in water swam more rapidly than did their siblings raised on land. The aquatic-raised snakes averaged 26% faster in burst swimming speed in absolute terms (cm per second – $F_{1,15} = 31·73$; $P < 0·0001$) and 21% faster relative to body length (i.e. number of body lengths swam per second; see Fig. 1 upper panel).

BURST CRAWLING SPEEDS

When tested on the terrestrial runway, snakes raised under terrestrial conditions sprinted more rapidly than did their siblings raised in an aquatic environment. This difference between the groups was significant both for absolute crawling speed (by 36%; $F_{1,13} = 10·88$; $P < 0·006$) and speed relative to body length (by 31%; see Fig. 1, lower panel).

NON-FORCED SWIMMING TRIALS

Neither the total distance swum around the circular track (cm; $F_{1,13} = 2·18$; $P = 0·16$; BL swum; $F_{1,13} = 2·76$; $P = 0·12$) nor the percentage of activity in the water differed significantly between the two groups ($F_{1,13} = 0·21$; $P = 0·65$). Nevertheless, non-forced swimming speed was much higher in the aquatic group in absolute terms (by 87%; $F_{1,13} = 7·46$; $P < 0·017$) as well as relative to body length (by 77%; $F_{1,13} = 8·98$; $P < 0·001$).

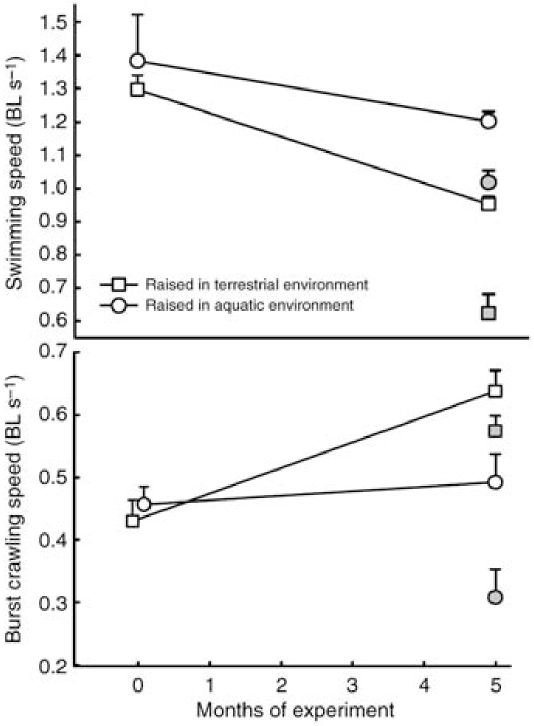

Fig. 1. Effect of prior experience (being raised in aquatic *vs* terrestrial environments) on locomotor performance in young tigersnakes. Twenty young snakes were reared either in aquatic (circles) or in terrestrial environments (squares). After 5 months of treatment, the aquatic-reared snakes (white circles) proved faster in burst swimming than their siblings raised in a terrestrial environment (white squares) (top panel; body lengths swam per s; $F_{1,15} = 48{\cdot}58$; $P < 0{\cdot}0001$). In contrast, the latter snakes crawled more rapidly when tested on land (lower panel; $F_{1,13} = 7{\cdot}82$; $P < 0{\cdot}016$). Having prey in the stomach significantly decreased burst swimming speed by 15% in the aquatic group (grey circles) *vs* 35% in the terrestrial group (grey squares; Repeated measures ANOVA; Wilks $\lambda = 0{\cdot}21$; $P < 0{\cdot}0001$; interaction $F_{1,15} = 9{\cdot}71$; $P < 0{\cdot}007$); and crawling speed by 10% the terrestrial group *vs* 38% in the aquatic group (Wilks $\lambda = 0{\cdot}08$; $P = 0{\cdot}0001$; interaction $F_{1,13} = 48{\cdot}85$; $P < 0{\cdot}0001$). Means speed values (in body length per second) + SEs are plotted.

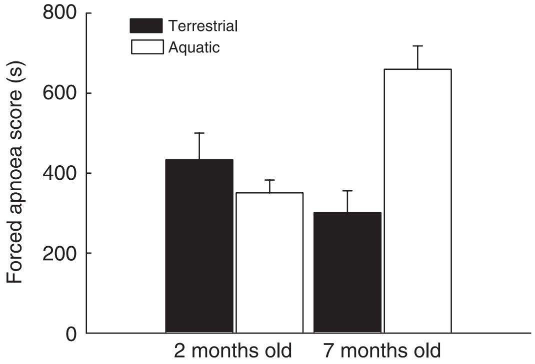

Fig. 2. The effect of rearing environment (aquatic *vs* terrestrial) on forced apnoea scores in young tigersnakes. Snakes that had been raised in an aquatic environment (white bars) stayed underwater for much longer than did their terrestrial-raised siblings (black bars; $F_{1,11} = 16{\cdot}65$; $P < 0{\cdot}0018$).

APNOEA SCORES

Free apnoea scores (i.e. voluntary dive durations) were similar between the two groups at the end of the experiment ($F_{1,13} = 0{\cdot}13$; $P = 0{\cdot}73$), but when threatened, the aquatic-raised group remained underwater for an average of 119% longer (see Fig. 2; $F_{1,13} = 15{\cdot}62$; $P < 0{\cdot}0017$).

EFFECT OF A FULL STOMACH ON LOCOMOTOR PERFORMANCE

In both experiments involving recently-fed snakes, prey mass did not differ significantly between the aquatic and terrestrial groups (on average, 31% of snake body mass; both $P > 0{\cdot}44$). The presence of prey in the stomach significantly decreased burst crawling speed, and did so to a greater extent in the aquatic group than in the terrestrial group (see Fig. 1 upper panel). In contrast, having prey in the stomach affected burst swimming speed more in the terrestrial group than in the aquatic group (see Fig. 1 lower panel). Lastly, having prey in the stomach strongly reduced apnoea scores in both treatments. The effect was greater in the aquatic group (71% reduction) than the terrestrial group (42%), because all recently-fed snakes showed similar, low durations of forced apnoea whereas the duration of forced dives in unfed animals was much greater in the aquatic than the terrestrial animals (Repeated measures ANOVA; Wilks' $\lambda = 0{\cdot}43$; $P < 0{\cdot}007$; interaction $F_{1,13} = 10{\cdot}13$; $P < 0{\cdot}007$). Thus, in this respect the advantages afforded by familiarity with aquatic habitats were evident for unfed but not fed snakes.

Discussion

The habitat in which a young tigersnake spent the first few months of its life affected its locomotor abilities, and did so to a surprising degree. A clear trade-off was apparent between locomotor abilities in the two habitat types: improved swimming/diving abilities entailed a decrease in terrestrial performances, and *vice versa*. This pattern is consistent with the notion that aquatic and terrestrial environments impose different constraints on the optimal morpho-functional attributes of locomotion (Jayne 1982, 1985), to the extent that muscle structures that optimize swimming in snakes differ from those that optimize terrestrial movement (Jayne 1982). Hence, we would expect to see trade-offs between these traits during ontogeny (Jayne 1982). Importantly, our animals were reared in two discrete environments (aquatic or terrestrial) so no compromise was offered. Most natural environments provide a more variable situation, favouring a combination of crawling and swimming (as is the case in Herdsman Lake). Presumably, such a situation favours (and induces?) phenotypes that strike a balance that minimizes costs and maximizes benefits in both environments. Nonetheless, such compromises may be constrained because swimming and crawling in snakes make conflicting demands on morphology (Jayne 1985).

Our study suggests that phenotypic plasticity: (i) may enhance organismal fitness by modifying mean locomotor speeds in each environment (as previously reported in other systems: e.g. Losos *et al.* 2000); and (ii) also, can lower some costs associated with day-to-day activities. The presence of a prey item in the stomach impairs locomotion in snakes both in terrestrial locomotion (Garland & Arnold 1983; Ford & Shuttlesworth 1986) and in aquatic locomotion (Shine & Shetty 2001). In keeping with this conclusion, snakes that contained freshly-ingested prey items in our study were slower in terms of crawling speed as well as swimming speed. However, the degree of impairment differed between treatment groups, suggesting that the 'costs' of a full stomach are manifested differently depending upon the kind of environment that the young animals had experienced prior to testing.

Flexibility of this kind is likely to confer strong fitness benefits to tigersnakes in nature. We do not know whether locomotor speed affects survival or growth rates in tigersnakes, although such a link has been documented in a field study of another snake species (Jayne & Bennett 1990). There is massive spatial and temporal heterogeneity of habitat types – especially, the proportion of the local area that is underwater – across much of the range occupied by tigersnakes. On a spatial scale, the swampy habitats occupied by this species consist of complex mosaics of water and land; given the relatively small home ranges of these animals (Shine 1979; X. Bonnet, unpublished data), animals in adjacent home ranges may well differ substantially in the proportion of their time spent either on land or in the water. On a temporal scale, the stochastic precipitation schedules characteristic of many Australian habitats mean that a high proportion of waterbodies are ephemeral, varying enormously in the extent of inundation from one year to the next (Flannery 2002). For example, Lake George near Canberra in the southern highlands of New South Wales has long been renowned for its high tigersnake densities (e.g. Worrell 1972). Its area commonly varies between 130 and 155 km^2 in area but over the last 200 years the lake has been almost completely dry on six occasions, sometimes for decades at a time (Department of Land and Water Conservation NSW 1999). Thus, a tigersnake born into such a population might encounter either dry conditions or very wet ones. Genetically-based adaptive processes cannot track such rapid, stochastic fluctuations, but adaptive plasticity is ideally suited to this challenge (Robinson & Dukas 1999). By facultatively adjusting locomotor performance to the conditions experienced during early life, each cohort of young tigersnakes can be well-matched to the habitats that they encounter.

In turn, plasticity in response to spatially and temporally heterogeneous precipitation regimes may have played a significant role in pre-adapting tigersnakes or related taxa to invasion of the oceans. For example, enhanced aquatic locomotor ability may have allowed snakes to spend more time underwater, where selective pressures associated with aquatic life could operate. Simultaneously, the impaired terrestrial locomotor performance of these animals may have forced them towards more highly aquatic habits, essentially driving a unidirectional progression of increasing dependence on aquatic life. Under this scenario, phenotypic plasticity induced by a specific habitat creates phenotypes that function best in that habitat; and in turn, tends to favour individuals that spend more of their time in that habitat. This 'ratchet' mechanism could plausibly accelerate the speed of an evolutionary transition to aquatic life (by disadvantaging individuals that tended to revert to more terrestrial [ancestral] habitats) and might also make such a transition more likely. The initial phases of the transition from land to water presumably occurred in coastal swamps, with some populations exploiting the abundant food resources available underwater in such habitats. By facilitating aquatic locomotion during foraging bouts (and perhaps for predator evasion also), adaptive plasticity of locomotor traits provided an opportunity for selection to operate on genetically-coded traits (i.e. genetic assimilation – Pigliucci & Murren 2003; Pigliucci *et al.* 2006) and speed up evolution (Behera & Nanjundiah 1997, 2004) that may ultimately have enabled more effective occupancy of oceanic habitats (Heatwole 1999; Shine & Shetty 2001; Shine *et al.* 2003).

We do not understand the proximate mechanisms that underlie the plastic responses in locomotor performances exhibited by juvenile tigersnakes, and future work may allow a better understanding of the potential physiological and morphological changes involved (e.g. in muscle structure). Future work also could investigate the time course of this response, and the persistence and reversibility of these changes in locomotor performances. Regardless of such issues, plasticity in locomotor performance in response to local conditions may well provide advantages in terms of organismal fitness. Although it is impossible to know if ancestral proto-seasnakes displayed either behavioural or morphological plasticity in locomotor performance, the widespread occurrence of phenotypic plasticity in living organisms lends credence to the suggestion (Bell 1997; Pigliucci 2001). Because our study organism is closely related to ancestral taxa that gave rise to the hydrophiid sea-snakes, similar plasticity may well have played an important role in pre-adapting these animals to the invasion of a new habitat type that posed novel locomotor challenges. Analogous work on other taxa in similarly critical phylogenetic positions should be feasible, and could help to answer the more general question of whether adaptive plasticity has influenced the rates or routes of major evolutionary radiations (Pigliucci & Murren 2003; West-Eberhard 2003).

Acknowledgements

We thank the region Poitou-charentes (France), the Conseil Général des Deux-Sèvres, and the University of Western Australia for funding. We also thank Don Bradshaw, Wally Gibb and David Pearson. Zoé Lechat helped with the feeding of the animals. The Animal Ethics Committee of UWA approved all procedures (permit 01/100/177) and the Department of Conservation and Land Management (WA; permit CE000347) issued fauna collection permits. Manuscript preparation was supported by the Australian Research Council.

References

Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* **294**, 321–326.

Aubret, F. (2004) Aquatic locomotion and behaviour in two disjunct populations of Western Australian Tiger snakes, *Notechis ater occidentalis*. *The Australian Journal of Zoology* **52**, 357–368.

Aubret, F., Bonnet, X., Shine, R. & Maumelat, S. (2004c) Swimming and pregnancy in Tiger snakes, *Notechis scutatus*. *Amphibia–Reptilia* **26**, 396–400.

Aubret, F., Maumelat, S., Bonnet, X., Bradshaw, S.D. & Schwaner, T. (2004b) Diet divergence, jaw size and scale counts in two neighbouring populations of Tiger snakes (*Notechis scutatus*). *Amphibia–Reptilia* **25**, 9–17.

Aubret, F., Shine, R. & Bonnet, X. (2004a) Adaptive developmental plasticity in snakes. *Nature* **431**, 261–262.

Baldwin, J.M. (1896) A new factor in evolution. *The American Naturalist* **30**, 441–451, 536–553.

Behera, N. & Nanjundiah, V. (1997) Transgene regulation in adaptive evolution: a genetic algorithm model. *Journal of Theoretical Biology* **188**, 153–162.

Behera, N. & Nanjundiah, V. (2004) Phenotypic plasticity can potentiate rapid evolutionary change. *Journal of Theorical Biology* **226**, 177–184.

Bell, G. (1997) Experimental evolution in *Chlamydomonas*. I. Short-term selection in uniform and diverse environments. *Heredity* **78**, 490–497.

Bonnet, X., Aubret, F., Lourdais, O., Ladyman, M., Bradshaw, S.D. & Maumelat, S. (2004) Do 'quiet' places make animals placid? Island *versus* mainland Tiger snakes. *Ethology* **11**, 573–592.

Bonnet, X., Bradshaw, S.D., Shine, R. & Pearson, D. (1999) Why do snakes have eyes? The (non-)effect of blindness in island tiger snakes (*Notechis scutatus*). *Behavioral Ecology and Sociobioliology* **46**, 267–272.

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O. & Bradshaw, S.D. (2002) 'Heaven' for serpents? A mark–recapture study of Tiger Snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecology* **27**, 442–450.

Bronmark, C. & Miner, J.G. (1992) Predator-induced phenotypical change in body morphology in crucian carp. *Science* **258**, 1348–1350.

Bull, J.J. (1980) Sex determination in reptiles. *Quarterly Review of Biology* **55**, 3–21.

Cogger, H.G. (1992) *Reptiles and Amphibians of Australia*. Reed Books, Cornell University Press.

Crews, D. (1994) Temperature, steroids and sex determination. *Journal of Endocrinology* **142**, 1–8.

Department of Land and Water Conservation (1999) *Annual Report 1998/99*. DLWC, Sydney.

Dudley, S.A. & Schmitt, J. (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *The American Naturalist* **147**, 445–465.

Flannery, T. (2002) *The Future Eaters: An Ecological History of the Australasian Lands and People*. Paperback, Grove Press.

Ford, N.B. & Shuttlesworth G.A. (1986) Effects of variations in food intake on locomotory performance of juvenile garter snakes. *Copeia* **1986**, 999–1001.

Garland, T. & Arnold, S.J. (1983) Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* **1983**, 1092–1096.

Garland T.Jr & Kelly S.A. (2006) Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology* **209**, 2344–2361.

Gravilets, S., Li, H. & Vose, M.D. (1998) Rapid parapatric speciation on holey adaptive landscapes. *Proceedings of the Royal Society of London B* **265**, 1483–1489.

Greene, E. (1989) A diet-induced developmental polymorphism in a caterpillar. *Science* **243**, 643–646.

Heatwole, H.F. (1999) *Sea Snakes*. University of NSW Press, Sydney.

Holway, D.A. & Suarez A.V. (1999) Animal behavior: an essential component of invasion biology. *Trends in Ecology and Evolution* **14**, 328–330.

Jayne, B.C. (1982) Comparative morphology of the semispinalis–spinalis muscle of snakes and correlations with locomotion and constriction. *Journal of Morphology* **172**, 83–96.

Jayne, B.C. (1985) Swimming in constricting (*Elaphe g. guttata*) and non constricting (*Nerodia pictiventris*) colubrid snakes. *Copeia* **1985**, 195–208.

Jayne, B.C. & Bennett A.F. (1990) The energetic cost of limbless locomotion. *Science* **249**, 524–527.

Keogh, J.S. (1998) Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society* **63**, 177–203.

Ladyman, M. & Bradshaw, S.D. (2003) The influence of dehydration on the thermal preferences of the Western Tiger snake, *Notechis scutatus*. *Journal of Comparative physiology B* **173**, 239–246.

Leclaire, M. & Brandle, R. (1994) Phenotypic plasticity and nutrition in a phytophagous insect – consequences of colonizing a new host. *Oecologia* **100**, 379–385.

Levin, D.A. (1988) Plasticity, canalization and evolutionary stasis in plants. *Plant Population Biology* (eds A. J. Davy, M. J. Hutchings & A. R. Watkinson), pp. 35–45 Blackwell, Oxford.

Losos, J.B., Creer, D.A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., Haskell, N., Taylor, P. & Ettling, J. (2000) Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* **54**, 301–305.

Mell, R. (1929) *Beitrage zur Fauna Sinica. IV. Grundzuge einer ökologie der chinesischen reptilien und einer herpetologischen tiergeographie Chinas*. Walter de Gruyter, Berlin.

Mirtschin, P. & Davis, R. (1992) *Snakes of Australia: Dangerous and Harmless*. Hill of Content Publishing, Melbourne.

Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. The Johns Hopkins University Press, Baltimore.

Pigliucci, M. & Murren, C.J. (2003) Genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? *Evolution* **57**, 1455–1464.

Pigliucci, M., Murran, C.J. & Schlichting, C.D. (2006) Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimenal Biology* **209**, 2362–2367.

Price, T.D., Qvarnstrom, A. & Irwin, D.E. (2003) The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London B* **270**, 1433–1440.

Robinson, B.W. & Dukas, R. (1999) The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos* **85**, 528–539.

Schlichting, C.D. & Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer, Sunderland.

Schwaner, T.D. & Sarre, S.D. (1988) Body size of tiger snakes in southern Australia, with particular reference to *Notechis ater serventyi* (Elapidae) on Chappell Island. *Journal of Herpetology* **22**, 24–33.

Sergeev, A.M. (1940) Researches in the viviparity of reptiles. *Moscow Society of Naturalists Jubilee Issue* 1–34.

Shine, R. (1979) Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetogica* **35**, 1–11.

Shine, R. (1983) Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* **57**, 397–405.

Shine, R. (1985) The evolution of viviparity in reptiles: an ecological analysis. *Biology of the Reptilia* (eds C. Gans & F. Billett), pp. 605–694 Wiley, New York.

Shine, R. (1987) Ecological comparisons of island and mainland populations of Australian Tiger snakes (*Notechis*: Elapidae). *Herpetologica* **43**, 233–240.

Shine, R. (1995) A new hypothesis for the evolution of viviparity in reptiles. *American Naturalist* **145**, 809–823.

Shine, R. (1999) Egg-laying reptiles in cold climates: determinants and consequences of nest temperatures in montane lizards. *Journal of Evolutionary Biology* **12**, 918–926.

Shine, R. (2004) Does viviparity evolve in cold climate reptiles because pregnant females maintain stable (not high) body temperatures? *Evolution* **58**, 1809–1818.

Shine, R. & Shetty, S. (2001) Moving in two worlds: aquatic and terrestrial locomotion in sea snakes (*Laticauda colubrina*, Laticaudidae). *Journal of Evolutionary Biology* **14**, 338–346.

Shine, R., Cogger, H.G., Reed, R.N., Shetty, S. & Bonnet, X. (2003) Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). *Journal of Zoology (London)* **259**, 261–268.

Shykoff, J.A. & Møller, A.P. (1999) Phenotypic plasticity of fluctuating asymmetry and fitness. *Oikos* **86**, 152–158.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology* **3**, 259–268.

Sultan, S.E. (1992) What has survived of Darwin's theory? *Evolutionary Trends in Plants* **6**, 61–71.

Waddington, C.H. (1942) Canalization of development and the inheritence of acquired characters. *Nature* **150**, 563.

Waddington, C.H. (1961) Genetic assimilation. *Advances in Genetics* **10**, 257–290.

Werner, E.E. (1986) Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *The American Naturalist* **128**, 319–341.

West-Eberhard, M.J (1989) Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**, 249–278.

West-Eberhard, M.J. (2003) *Development Plasticity and Evolution*. Oxford University Press, Oxford.

Whitlock, M. (1996) The heritability of fluctuating asymmetry and the genetic control of developmental stability. *Proceedings of the Royal Society of London B* **263**, 849–854.

Wimberger, P.H. (1994) Trophic polymorphisms, plasticity, and speciation in vertebrates. *Theory and Application of Fish Marine Science* (eds D.J. Stouder, K.L. Fresh & R.J. Feller), pp. 19–43 University of South Carolina Press, Columbia.

Woltereck, R. (1909) Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphnien. *Verhandlungen der deutschen zoologischen Gesellschaft* **19**, 110–173.

Worrell, E.G. (1972) *Dangerous Snakes of Australia and New Guinea*. Angus and Robertson, Sydney.

Yeh, P.J. & Price T.D. (2004) Adaptive phenotypic plasticity and the successful colonization of a novel environment. *The American Naturalist* **164**, 531–542.

Received 29 December 2006; accepted 2 June 2007
Editor: Jeffrey Walker