

## Fitness costs may explain the post-colonisation erosion of phenotypic plasticity

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### SUMMARY

Many organisms can adjust their phenotypes to match local environmental conditions *via* shifts in developmental trajectories, rather than relying on changes in gene frequencies wrought by natural selection. Adaptive developmental plasticity confers obvious benefits in terms of rapid response and higher mean fitness, so why is it not more common? Plausibly, adaptive plasticity also confers a cost; reshaping the phenotype takes time and energy, so that canalised control of trait values enhances fitness if the optimal phenotype remains the same from one generation to the next. Although this idea is central to interpreting the fitness consequences of adaptive plasticity, empirical data on costs of plasticity are scarce. In Australian tiger snakes, larger relative head size enhances maximal ingestible prey size on islands containing large prey. The trait arises *via* adaptive plasticity in snake populations on newly colonised islands but becomes genetically canalised on islands where snakes have been present for much longer periods. We experimentally manipulated relative head size in captive neonatal snakes to quantify the costs of adaptive plasticity. Although small-headed snakes were able to increase their head sizes when offered large prey, the delay in doing so, and their inability to consume large prey at the outset, significantly reduced their growth rates relative to conspecifics with larger heads at the beginning of the experiment. This study describes a proximate cause to the post-colonisation erosion of developmental plasticity recorded in tiger snake populations.

Key words: phenotypic plasticity, cost, body size, swallowing, prey, snake.

### INTRODUCTION

Phenotypically plastic organisms display alternative phenotypes in different environments, and thus can adopt fitness-enhancing modifications of their phenotypic traits in response to the challenges exerted by local environments (Stearns, 1989; West-Eberhard, 2003). Such modifications can occur more rapidly than if phenotypic traits were hard-wired (canalised) genetically, because in the latter situation the changes can occur only from one generation to the next (Futuyma, 2005). Why, then, are so many phenotypic traits determined by genetic factors alone, with little adaptive flexibility in expression depending upon the local environments encountered by the organism?

Theory suggests that the answer lies in the costs (and limits) as well as in the benefits of plasticity (Behera, 1994; Mayley, 1997; De Witt et al., 1998; Pigliucci, 2005; Pigliucci et al., 2006). Thus, in the absence of unpredictable variation in optimal trait values, canalised mechanisms can generate the optimal phenotype without incurring 'costs' associated with plasticity *per se*. Costs of plasticity are defined as a decrease in fitness even when an optimal phenotype is expressed by plasticity (Pigliucci, 2005). Such costs can extend beyond the cost of producing an alternative phenotype and might include developmental instability and/or the time and energy required for the organism to detect the relevant pressure (Pigliucci, 2001; Relyea, 2002) and respond adaptively to it *via* phenotypic modification (De Witt et al., 1998). Although the concept that adaptive plasticity may confer costs as well as benefits is central to this body of theory, empirical measurement of such costs largely has lagged behind conceptual work (but see Krebs and Feder, 1997; Relyea, 2002; Bashey, 2006; Weining et al., 2006; Steiner and Buskirk, 2008).

Adaptive phenotypic plasticity can play a decisive role in the success of a species invading a novel environment (Ehrlich, 1989;

Holway and Suarez, 1999; Yeh and Price, 2004). In the case of Australian tiger snakes (*Notechis scutatus*, Elapidae), colonising small offshore islands containing breeding seabird populations, there is intense selection for an increase in relative head size of neonatal snakes (Aubret et al., 2004a). Larger head size increases maximum ingestible prey size in these gape-limited predators, and may be critical to a young snake's ability to feed (King, 2002). As expected, island tiger snakes tend to have larger heads than their mainland progenitors (Aubret et al., 2004a; Aubret et al., 2004b) – but this increase is achieved *via* different mechanisms on islands that have been recently colonised by snakes compared with islands where the snakes have been present for many thousands of years (Keogh et al., 2005; Aubret and Shine, 2009). On recently colonised islands, the increased head size is achieved *via* adaptive plasticity, with larger prey size stimulating an increase in relative head size (Aubret et al., 2004a). By contrast, neonates in long-established island populations have larger relative head sizes at birth, and little adaptive plasticity in this trait (Aubret and Shine, 2009). Plausibly, this transition from a dependence on developmental plasticity to canalisation reflects some costs and limits associated with plasticity. That is, a consistent (among generation) selective advantage to large head size favours genes that produce this phenotype irrespective of the nutritional environment, because the alternative pathway (plasticity) necessarily means that the young snake will not attain the optimal phenotype until after some (perhaps prolonged) period of growth, during which time it will be unable to ingest large prey items.

To assess this putative cost of plasticity, we can compare swallowing abilities and growth rates between two groups of snakes: those with large heads from birth, and those that develop large heads *via* adaptive plasticity in the course of early life. Any such comparison must closely match the individuals involved for

all other traits, so inter-population comparisons are inappropriate; too many other differences (in intrinsic growth rates, head morphology, etc.) could mask the effects of divergent growth trajectories in head size. Hence, we experimentally created the two phenotypes (large head with no plasticity *versus* small head with plasticity) from a single population, mimicking the early *versus* older stages of a colonisation event (Aubret and Shine, 2009). We raised sibling neonatal snakes from a recently colonised island [the highly plastic population of Carnac Island, Australia (Aubret and Shine, 2009)] either on small or large prey items, to generate two groups of same-sized snakes with different head sizes (one with large heads and one with small heads). From this point (the beginning of the main experiment), all snakes were given very large prey items only. The new diet thus induced plasticity in head development in the initially small-headed snakes but not in the initially larger-headed animals (i.e. for which the developmental limit of plasticity in head size was reached). This design allowed us to compare the 'fitness' (measured by swallowing success and subsequent growth rate) of two alternative genotypes producing a similar phenotype either by plasticity or *via* canalised genes (at birth). Any advantage to the latter group would provide a direct measurement of costs associated with adaptive developmental plasticity.

However, this experimental design also created another difference between the small-prey (SP) group and the large-prey (LP) group; the latter not only had larger heads, but also had the experience of encountering larger prey (and thus, plausibly, might have been better

able to swallow a large prey item because of that experience and not simply because of their larger head sizes). To test for such an effect, we repeated the experiment using snakes from a population with very low (undetectable) plasticity for head sizes [Tasmania (Aubret and Shine, 2009)] in order to generate snakes differing in prior exposure to large prey but not in head sizes.

## MATERIALS AND METHODS

### Study species and specimen collection

The experiment was run over three reproductive seasons under the same laboratory conditions (2006, 2007, 2008). Carnac Island neonates were born to eight pregnant female Australian tiger snakes (*N. scutatus* Peters 1861) captured on Carnac Island (32°07'17"S; 115°39'43"E; 12 km off the coast of Fremantle, Western Australia) in February 2006 (three females) and February 2007 (five females). A total of 137 neonates were born in March and April of 2006 and 2007. Litter size averaged 17.0±5.5 live neonates. Another four pregnant female tiger snakes were captured in Tasmania (41°09'49"S; 146°10'17"E) in March 2008. A total of 82 Tasmania neonates were born in March and April 2008 (litters averaged 21±6.38 live neonates).

Within a week of capture, all females were flown to the laboratory (University of Sydney) where they were housed until parturition in individual cages (50 cm × 40 cm × 30 cm), containing pine wood shavings as substratum, a water dish and shelter. Water was available *ad libitum* and food (dead mice) was offered once a week.

Table 1. Morphological traits of Australian tiger snakes (*Notechis scutatus*) raised on either small or large food items (to generate disparity in relative head size *via* developmental plasticity), then offered large prey items only

	Small headed N=17 <b>N=13</b>	Large headed N=17 <b>N=13</b>	d.f.; F	P
Start of experiment part 1				
Body mass (g)	6.39±0.82 <b>4.57±0.54</b>	6.42±0.88 <b>4.71±0.53</b>	1, 32; 0.01 <b>1, 24; 0.44</b>	0.91 <b>0.51</b>
Snout-vent length (cm)	19.97±1.03 <b>20.30±1.11</b>	19.79±1.19 <b>20.48±0.71</b>	1, 32; 0.23 <b>1, 24; 0.30</b>	0.63 <b>0.59</b>
Body condition*	6.39±0.82 <b>4.61±0.54</b>	6.46±0.88 <b>4.67±0.53</b>	1, 31; 0.24 <b>1, 23; 0.15</b>	0.63 <b>0.70</b>
Skull length (mm)	12.99±0.23 <b>11.89±0.26</b>	12.82±0.46 <b>11.96±0.29</b>	1, 32; 1.93 <b>1, 24; 0.43</b>	0.17 <b>0.52</b>
Jaw length (mm)	14.71±0.42 <b>13.40±0.28</b>	14.71±0.44 <b>13.49±0.26</b>	1, 32; 0.01 <b>1, 24; 0.77</b>	0.93 <b>0.39</b>
Head width (mm)	5.81±0.20 <b>5.69±0.21</b>	5.82±0.20 <b>5.61±0.22</b>	1, 32; 0.07 <b>1, 24; 0.79</b>	0.80 <b>0.39</b>
Inter-nostril width (mm)	3.58±0.21 <b>3.41±0.16</b>	3.55±0.20 <b>3.51±0.13</b>	1, 32; 0.19 <b>1, 24; 3.17</b>	0.66 <b>0.09</b>
Eye diameter (mm)	2.58±0.16 <b>2.76±0.17</b>	2.56±0.15 <b>2.75±0.17</b>	1, 32; 0.11 <b>1, 24; 0.10</b>	0.73 <b>0.75</b>
Fang length (mm)	1.51±0.10 <b>1.58±0.12</b>	1.55±0.11 <b>1.57±0.12</b>	1, 32; 0.98 <b>1, 24; 0.07</b>	0.33 <b>0.80</b>
Start of experiment part 2				
Body mass (g)	19.10±2.54 <b>12.41±1.90</b>	20.01±3.34 <b>15.01±2.89</b>	1, 32; 0.71 <b>1, 24; 7.00</b>	0.40 <b>0.014</b>
Snout-vent length (cm)	31.87±1.90 <b>31.92±1.73</b>	32.54±2.37 <b>33.34±1.72</b>	1, 32; 0.75 <b>1, 24; 4.41</b>	0.39 <b>0.046</b>
Body condition*	19.45±2.54 <b>13.29±1.90</b>	19.66±3.34 <b>14.14±2.89</b>	1, 31; 0.09 <b>1, 23; 2.41</b>	0.77 <b>0.14</b>
Skull length (mm)	14.71±0.56 <b>14.18±0.31</b>	15.52±0.41 <b>14.33±0.55</b>	1, 32; 23.11 <b>1, 23; 1.47</b>	0.0001 <b>0.24</b>
Jaw length (mm)	16.94±0.50 <b>16.20±0.37</b>	18.29±0.47 <b>16.41±0.71</b>	1, 32; 64.05 <b>1, 23; 1.56</b>	0.0001 <b>0.23</b>
Head width (mm)	6.62±0.14 <b>6.57±0.19</b>	6.87±0.29 <b>6.71±0.29</b>	1, 32; 9.46 <b>1, 23; 2.58</b>	0.004 <b>0.12</b>
Inter-nostril width (mm)	4.12±0.15 <b>4.22±0.18</b>	4.30±0.21 <b>4.26±0.23</b>	1, 32; 7.22 <b>1, 23; 0.27</b>	0.001 <b>0.61</b>
Eye diameter (mm)	3.15±0.12 <b>3.26±0.13</b>	3.23±0.16 <b>3.28±0.18</b>	1, 32; 2.27 <b>1, 23; 0.03</b>	0.14 <b>0.86</b>
Fang length (mm)	2.33±0.12 <b>2.08±0.09</b>	2.52±0.23 <b>2.14±0.12</b>	1, 32; 8.62 <b>1, 23; 1.97</b>	0.006 <b>0.17</b>
End of experiment				
Body mass (g)	22.90±5.17	29.22±6.37	1, 32; 10.01	0.003
Snout-vent length (cm)	33.91±2.59	36.59±2.54	1, 32; 9.29	0.005
Body condition*	25.58±5.17	26.54±6.37	1, 31; 0.02	0.90
Skull length (mm)	15.39±0.69	16.07±0.50	1, 32; 11.00	0.002
Jaw length (mm)	18.35±0.77	19.38±0.77	1, 32; 15.20	0.0005
Head width (mm)	7.02±0.31	7.17±0.38	1, 32; 1.63	0.21
Inter-nostril width (mm)	4.38±0.26	4.58±0.31	1, 32; 3.74	0.062
Eye diameter (mm)	3.27±0.24	3.36±0.20	1, 32; 1.35	0.25
Fang length (mm)	2.45±0.16	2.65±0.22	1, 32; 9.05	0.005

The table shows sizes of snakes at birth, at the end of the first period (when divergence in relative head size had been generated) and then after the end of the second phase, when only large prey items were provided. Mean values, associated standard deviations and statistical results are given for Carnac Island (regular font) and Tasmanian (bold font) tiger snakes. Head measurements were snout-vent length corrected for Tasmanian snakes (part 2) to account for snout-vent length heterogeneity between the two treatment groups. \*Body condition is snout-vent length corrected body mass.

A heat source provided basking opportunities (high pressure Na<sup>+</sup> lamp; 600 W). Ambient temperature was 27°C by day and 17°C at night.

#### Data collection

For each snake, the size and the shape of the head were measured with digital callipers ( $\pm 0.01$  mm) as follows: jaw length (from the tip of the snout to the quadrato-articular projection); skull length (from the tip of the snout to the base of the skull); head width (maximal width above the eyes, from the external margins of the supra-oculars); inter-nostril gap; eye diameter; and fang length. Body mass was recorded on a digital scale ( $\pm 0.1$  g) (Nutriflo Hydroponic Systems, West Gosford, NSW, Australia), and snout–vent length with a measuring tape ( $\pm 0.5$  cm) (Bunnings Warehouse, West Gosford, NSW, Australia). All measurements were performed by a single and highly experienced person, on a blind measurement design, using a standardised procedure to minimise measuring errors.

#### Part 1. Creating the phenotypic divergence

Less than 24 h after birth, neonates were sexed by eversion of the hemipenes, measured (snout–vent length,  $\pm 0.5$  cm) and weighed ( $\pm 0.1$  g). Young snakes were individually housed in plastic tubs (40 cm  $\times$  25 cm  $\times$  12 cm) in a similar way as their mothers. A heat source at one end of the tub provided basking opportunities. We selected 34 Carnac Island neonates and allocated them to two different groups (2  $\times$  17 snakes). Another 26 Tasmanian neonates were allocated to two different groups (2  $\times$  13 snakes). In both cases we used a split-clutch design to balance potential maternal effects. For each population, one group was fed small dead mice (SP, ranging from 1 g to 2.6 g throughout the experiment) and the other group larger items (LP, ranging from 1.1 g to 11.2 g).

#### Part 2. Costs of developmental plasticity

##### Carnac Island

From day 255 onwards, we changed the diet of both groups, offering large to very large prey items. All snakes were offered food once a week, beginning with prey averaging 46.7% of snake body mass (first feed), then 95.9% (second feed) and finally 52.5% (third feed). If a snake failed to swallow its prey, it was given a small prey item (1.5–2 g) the next day to avoid starvation. Feeding trials were videotaped (JVC Hard-disk Camcorder, Gosford, NSW, Australia) to determine swallowing time and the number of jaw protractions used in prey handling during ingestion. A prey was considered successfully swallowed when its body was fully engaged in the snake

digestive track (past the rear of the snake's head) so that the snake was able to normally close its mouth (neglecting the prey's tail) and had resumed tongue flicking. This treatment terminated after 33 days, by which time small-headed juveniles snakes had expressed plasticity and developed jaws as large as those possessed by the large-headed animals at the beginning of this main experiment (see Results for details).

##### Tasmania

A similar procedure was followed with Tasmanian juveniles; snakes were first offered a large meal (32.77  $\pm$  7.02% of snake's body mass) and a second larger meal a week later (108.38  $\pm$  20.39% of snake's body mass). All data were log-transformed prior to analysis.

## RESULTS

### Part 1. Creating the phenotypic divergence

#### Carnac Island

Mean body sizes and head sizes were similar between the two groups at the start of the experiment (Table 1). The total amount of food consumed was similar between the SP and LP groups [47.97  $\pm$  3.42 g *versus* 48.74  $\pm$  7.44 g, respectively; analysis of variance (ANOVA)  $F_{1,32}=0.05$ ;  $P=0.83$ ] but items averaged larger in the LP group (1.73  $\pm$  0.05 g *versus* 4.02  $\pm$  0.74 g, respectively;  $F_{1,32}=246.70$ ;  $P<0.00001$ ). After 255 days of growth, the two groups exhibited similar mean body sizes but very different head sizes (Table 1).

#### Tasmania

SP and LP groups were similar in body and head sizes at the start of the experiment (Table 1). The total amount of food consumed was similar between the SP and LP groups (48.46  $\pm$  0.41 g *versus* 48.38  $\pm$  0.48 g, respectively; ANOVA  $F_{1,24}=0.23$ ;  $P=0.63$ ) but items averaged larger in the LP group (1.68  $\pm$  0.05 g *versus* 3.08  $\pm$  0.69 g, respectively;  $F_{1,24}=53.77$ ;  $P<0.00001$ ). At the end of the 255-day feeding period, relative head size did not significantly differ between the SP and LP treatment groups for any of the variables measured: skull length, jaw length, head width, inter-nostril width, eye diameter and fang length (Table 1).

### Part 2. Costs of developmental plasticity

#### Carnac Island

Large-headed snakes were more capable of swallowing large prey items (see Table 2). They did so faster (Fig. 1) and with fewer jaw protractions than did their smaller-headed siblings. In turn, the large-headed snakes grew more rapidly in body mass and snout–vent

Table 2. Swallowing success (proportion of items successfully ingested) of two groups of Australian tiger snakes (*Notechis scutatus*) offered large food items

	Small headed $N=17$ <b><math>N=13</math></b>	Large headed $N=17$ <b><math>N=13</math></b>	d.f.; $F(\chi^2)$	$P$
First feed				
Prey mass (g)	9.03 $\pm$ 2.04 <b>3.98 <math>\pm</math> 0.30</b>	9.02 $\pm$ 2.66 <b>3.96 <math>\pm</math> 0.42</b>	1, 32; 0.01 <b>1, 24; 0.01</b>	0.99 <b>0.92</b>
Swallowing success (%)	82.3 <b>100</b>	88.2 <b>100</b>	1; 0.23 –	0.63 –
Swallowing time (min)	30.39 $\pm$ 16.69 <b>15.68 <math>\pm</math> 4.11</b>	16.69 $\pm$ 11.48 <b>15.37 <math>\pm</math> 10.09</b>	1, 27; 5.34 <b>1, 24; 0.01</b>	0.029 <b>0.92</b>
Number of jaw protractions	206.14 $\pm$ 111.63 <b>116.92 <math>\pm</math> 24.45</b>	96.53 $\pm$ 30.31 <b>105.31 <math>\pm</math> 23.93</b>	1, 27; 24.04 <b>1, 24; 1.74</b>	0.0001 <b>0.20</b>
Second feed				
Prey mass (g)	18.67 $\pm$ 2.31 <b>16.57 <math>\pm</math> 1.81</b>	18.09 $\pm$ 2.94 <b>16.91 <math>\pm</math> 1.48</b>	1, 32; 0.51 <b>1, 17; 0.21</b>	0.48 <b>0.66</b>
Swallowing success (%)	11.7 <b>0</b>	52.9 <b>0</b>	1; 6.58 –	0.010 –
Third feed				
Prey mass (g)	11.90 $\pm$ 1.25	11.95 $\pm$ 2.96	1, 32; 0.01	0.94
Swallowing success (%)	52.9	64.7	1; 0.49	0.48

One group had previously been fed on small prey items (small headed), and one on large prey items (large headed), to generate disparity in relative head size via developmental plasticity. Mean values, associated standard deviations and statistical results are given for Carnac Island (regular font) and Tasmanian (bold font) tiger snakes

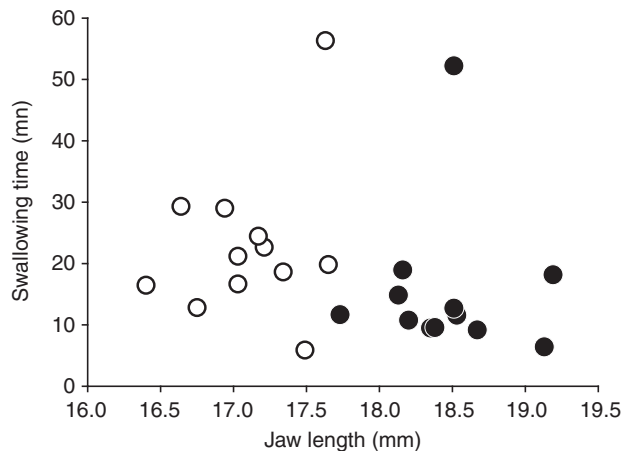


Fig. 1. Swallowing time as a function of jaw size in small-headed (open circles) and large-headed (black circles) 8 months old Carnac Island tiger snakes (Spearman rank order correlation:  $N=29$ ;  $R=-0.47$ ;  $t=-2.75$ ;  $P<0.011$ ).

length (see Fig. 2), and averaged 27.6% heavier and 7.9% longer than the small-headed group after 33 days of treatment (see Fig. 3). As predicted, the sudden switch to large prey items triggered developmental plasticity in the small-headed snakes: jaw lengths increased 85.5% faster than in the large-headed group (repeated-measures ANOVA  $F_{1,32}=7.09$ ;  $P<0.012$ ).

#### Tasmania

Snakes were first offered large dead mice representing on average  $32.77\pm 7.02\%$  of each snake's body mass (between treatments  $F_{1,24}=0.01$ ;  $P=0.94$ ; Table 2) and on a second feeding episode much larger dead mice (mean mass= $16.46\pm 1.96$  g; % of snake's body mass= $108.38\pm 20.39\%$ ; both  $P>0.16$ ). No significant differences in swallowing success, swallowing time and number of jaw protractions existed between the two treatment groups in either of the two feeding events (see Table 2). Swallowing success was 0% for the snakes raised on small prey and 10% for the snakes raised on large prey (Yates' corrected  $\chi^2$ ;  $P>0.99$ ). The mean time spent trying to swallow the prey was similar between the groups (on average  $22.36\pm 38.74$ ;  $F_{1,17}=0.09$ ;  $P=0.76$ ).

#### DISCUSSION

In the control (Tasmanian) snakes that lacked phenotypic plasticity in jaw sizes, prior exposure to large *versus* small prey had no significant effect on swallowing performance (i.e. no learning effect). By contrast, relatively larger-headed Carnac Island snakes swallowed large prey items more successfully and efficiently than did their smaller-headed conspecifics. In nature, the more rapid ingestion of prey by larger-headed snake may reduce the risks of predation. Small snakes are highly vulnerable while swallowing large prey, because their main weapons (jaws and fangs) are unavailable for predator defence over that period (Vincent et al., 2006).

In addition to this inferred 'cost' of a smaller head, our data demonstrate that developmental plasticity confers a fitness cost in terms of growth rates. Feeding small-headed Carnac Island snakes with large prey items triggered developmental plasticity in head size but it took approximately 33 days for these animals to develop jaws as large as those possessed by the large-headed animals at the beginning of the main experiment. This 'lag time' constitutes a cost to developmental plasticity, because the young snakes were unable

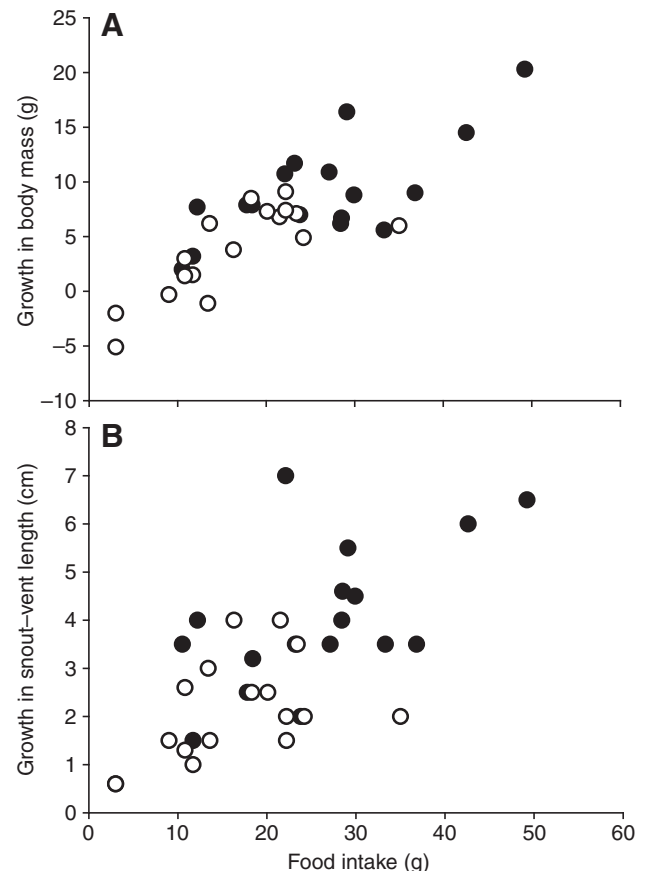


Fig. 2. Growth in body mass (A) and snout-vent length (B) as functions of food intake (Spearman rank order correlation:  $N=34$ ;  $R=0.68$ ;  $t=5.32$ ;  $P<0.0001$  and  $N=34$ ;  $R=0.60$ ;  $t=4.21$ ;  $P<0.0002$ , respectively) in small-headed (open circles) and large-headed juvenile Carnac Island tiger snakes (black circles).

to swallow larger prey (and hence, grow faster) until their heads grew large enough to do so. This accelerated growth may increase survival rate by reducing vulnerability to predation [risk of predation in reptiles is size-dependent (Ferguson and Fox, 1984; Forsman, 1993; Webb and Whiting, 2005)] and increasing feeding success (Forsman, 1996; King, 2002; Vincent and Mori, 2008) (present study). Additionally, there is a strong positive feedback involved: the larger a snake grows, the larger the prey items that it can ingest. Thus, size differentials generated early in life (by the costs of developmental plasticity, for example) may persist or even become amplified later in life. Ultimately, faster-growing snakes are likely to attain sexual maturity earlier (or at a larger body size) and/or increase litter size and/or egg size (Ford and Seigel, 1989; Beaupre et al., 1998; Rivas and Burghardt, 2001).

Our data thus support the notion that adaptive plasticity provides a selective advantage in the early stages of the colonising event; but that a consistent selective force for larger head size ultimately will result in replacement of the plasticity-based pathway with a canalised genetic basis for the trait (Pigliucci et al., 2006; Pigliucci and Murren, 2003; Lande, 2009; Aubret et al., 2009). In other words, the capacity to increase swallowing abilities *via* developmental plasticity is better (in terms of fitness) than not being able to do so; but over a longer period, this plastic solution may confer a disadvantage in feeding success compared with a canalised solution of the trait (i.e. being born with a large head instead). Under



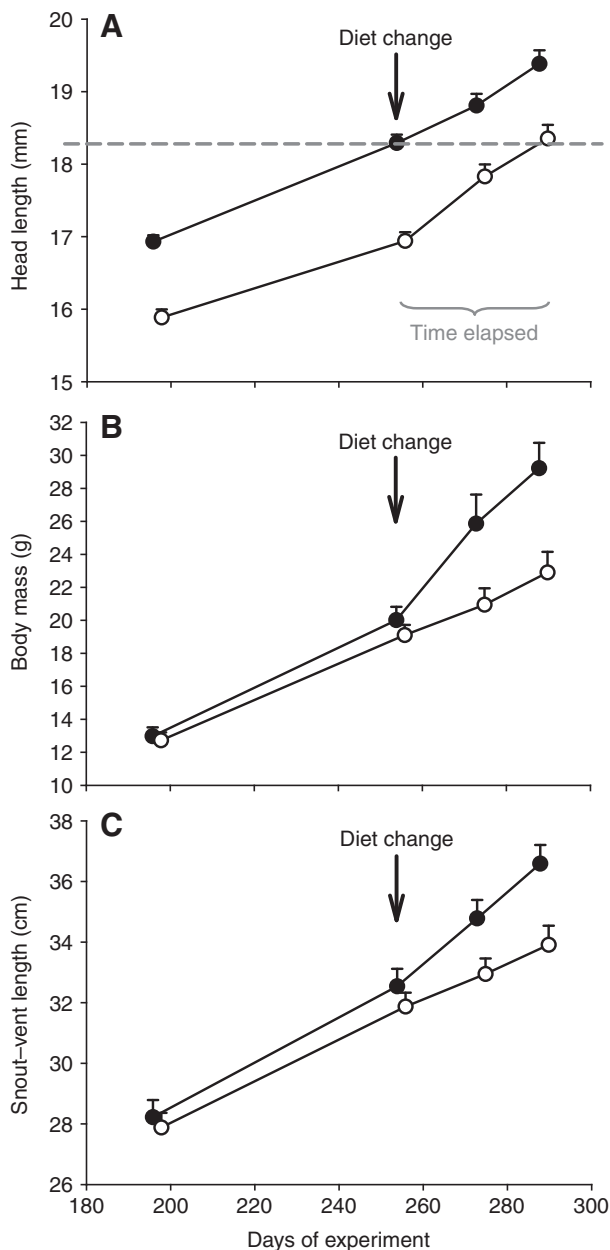


Fig. 3. Growth rates of two groups of Carnac Island tiger snakes in jaw size (A), body mass (B) and snout-vent length (C) during a 35-day period when they were offered large prey items. One group had previously been raised on small prey (open circles), and thus had relatively small heads that increased in response to the increased prey size (A). The other group had been raised on large prey (black circles) and thus had larger heads initially (A). Large-headed snakes were better able to swallow large prey and grew faster than the initially small-headed group in body mass (B) and snout-vent length (C). Mean values and associated standard errors are plotted.

such circumstances, theory predicts the evolutionary replacement of the plastic solution by a canalised solution (i.e. genetic assimilation). This scenario accords well with evolutionary transitions in isolated populations of tiger snakes across southern Australia, which demonstrates a progressive replacement of plasticity in head growth by large head size at birth along the colonisation timeframe (Aubret and Shine, 2009). The current study

thus provides strong support to both theoretical (Pigliucci et al., 2006; Lande, 2009) and empirical work (Aubret et al., 2004; Aubret and Shine, 2009).

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