Adaptive developmental plasticity in snakes

Genes and environment stretch snake jaws to meet the demands of prey size.

The morphology of organisms is generally well matched to their environment, presumably because expression of their genes is tailored either at the population or the individual level to suit local conditions: for example, snake populations that persistently encounter large prey may accumulate gene mutations that specify a large head size, or head growth may be increased in individual snakes to meet local demands (adaptive developmental plasticity)[1]. Here we test the relative contributions of genetics and environment to the jaw sizes of two tiger snake populations: one that consumes small prey on the mainland, and an island population that relies on larger prey and has a larger jaw size. Although the idea of adaptive plasticity in response to environmental pressures is controversial[2], we find that both factors influence the difference in jaw size between the two populations, and the influence of developmental plasticity is greater in the island population.

Snakes are ideally suited to our investigation because their jaw length constrains their maximal ingestible prey size and so reflects adaptation to local prey resources[3]. Tiger snakes (*Notechis scutatus*, Elapidae; Fig. 1) are viviparous Australian snakes[4]. We studied one mainland population (at Herdsman's Lake: 31° 55′ S, 115° 48′ E) and one island population 25 km away (Carnac Island: 32° 07′ S, 115° 39′ E). Adult mainland snakes feed on frogs and mice, whereas adult

Figure 1 On an island in southwestern Australia, tiger snakes feed mostly on the large chicks of silver gulls, rather than on the small frogs preyed upon by mainland populations.

island snakes mostly take silver-gull chicks (mean prey masses, 12 g compared with 30 g; circumference, 33 mm compared with 78 mm)[6]. In keeping with this dietary divergence, the island snakes grow larger and have larger heads relative to their body length[5,6].

To investigate whether this geographic divergence in relative head size is driven by genes that encode for head size or by the exposure of growing snakes to larger prey, we captured pregnant females in early summer and maintained them under laboratory conditions until they gave birth in the autumn. They were housed individually with access to water and a heat source, and given laboratory mice as food. Nine island females and thirteen mainland females gave birth to 123 and 129 neonates, respectively. We randomly selected one or two neonates from each litter and raised them under the same conditions as their mothers.

Half the neonates received large mice as prey, whereas the others were given the same total mass of smaller mice as prey: that is, mice fed to the two treatment groups differed in average prey mass ($F_{3,81} = 101.8$, $P<0.001$) and circumference ($F_{3,81} = 101.7$, $P<0.001$). The amount of food provided monthly was similar among the four groups of young snakes (island and mainland snakes, each fed either small or large prey; $F_{3,75} = 0.29$, $P = 0.84$), and led to similar growth trajectories in body mass ($F_{4,104} = 1.36$, $P = 0.25$) and snout–vent length ($F_{3,78} = 0.09$, $P = 0.96$). All snakes were measured for jaw and skull length on four occasions over 8 months using digital callipers (± 0.1 mm). The standardized husbandry conditions and split-clutch design should have minimized any maternal effects on offspring traits.

Head sizes were significantly plastic in Carnac Island juveniles with respect to skull

Figure 2 Relative jaw length of growing tiger snakes as a function of prey size. Neonatal snakes from the mainland (Herdsman's Lake; $n = 20$; squares) and from Carnac Island ($n = 19$; circles) were born and kept in captivity. The young snakes were fed weekly on mice. Within each group, half of the snakes were given large prey (mice, 1.8–5.0 g; 2.5–4.7 mm in circumference; filled symbols) and the other half received small prey (mice, 1.7–1.8 g; 2.3–2.5 mm; open symbols). Jaw size of island snakes exposed to large prey increases significantly more than for mainland snakes (mean values + s. d.).

length (results not shown; repeated measures MANOVA; Wilks' $\lambda = 0.41$, $P = 0.03$; interaction of time and prey size, $F_{3,45} = 3.10$, $P < 0.036$) and jaw length (Wilks' $\lambda = 0.25$, $P < 0.0015$; interaction $F_{3,45} = 19.15$, $P < 0.0001$); these effects were not evident in mainland juveniles (all $P > 0.24$) (Fig. 2). Exposure to larger prey therefore seems to increase the head size of the island snakes more than that of the mainland snakes (two-way ANOVA, with origin and treatment as factors and the successive measurements of jaw length as the repeated measure: interaction $F_{3,78} = 5.66, P < 0.0015$) (Fig. 2).

These results indicate that adaptation could be influenced both by genes encoding for head size and by developmental plasticity. First, neonates of island snakes had larger heads than mainland snakes, despite similar body sizes (ANCOVA with location as the factor, log body-length as the covariate, log jaw-length as the dependent variable: $F_{1,244} = 25.65$, $P < 0.001$). This geographic divergence is apparent at birth, so presumably reflects hard-wired genetic differences.

Second, the relative jaw sizes of island snakes fed on large prey rapidly increased relative to the jaws of their siblings fed on small prey, whereas the mainland snakes showed no such effect (Fig. 2). We conclude that island tiger snakes can consume larger prey than mainland conspecifics for two reasons: first, they may carry genes that determine a larger relative head size; and second, their head sizes enlarge facultatively if they eat large prey.

Our study demonstrates an important ecological role for adaptive plasticity, and highlights the impossibility of dividing phenotypic variation into simplistic categories of 'nature' and 'nurture'[7]. Tiger snakes are highly flexible predators that track prey resources by means of a complex adaptive response. This response involves not only hard-wired traits that match phenotype to differences in long-term average conditions, but also a developmentally plastic component that matches individuals within each generation to fluctuations in prey size.

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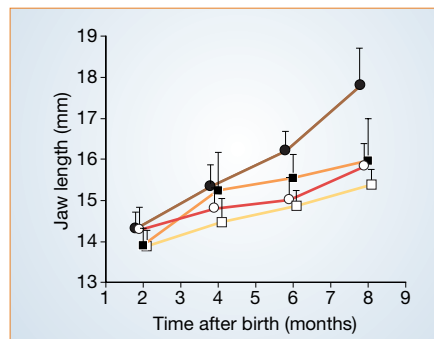§Biological Sciences A08, University of Sydney,

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Ecology

Ultraviolet reflectance by the skin of nestlings

Birds can perceive the reflectance of ultraviolet light by biological structures[1–5]. Here we show that the skin of the mouth and body of starling nestlings substantially reflects light in the ultraviolet range and that young in which this reflectance is reduced will gain less mass than controls, despite low background levels of ultraviolet and visible light in the nest. We suggest that this ultraviolet reflectance from starling nestlings and its contrast with surrounding surfaces are important for parental decisions about food allocation.

Reflectance of ultraviolet light in the 300–400-nanometre range from feathers, fruits, insects and vole scent marks is used by birds to make decisions about mate choice and food selection[1–5]. The function of ultraviolet reflectance by the brightly coloured skin of some birds is unknown[6,7], but it may play a role in parent–offspring communication[6].

The flanges (skin surrounding the mouth) in nestlings of both starlings (*Sturnus vulgaris*) and great tits (*Parus major*) is strongly reflective (Fig. 1a,c, respectively; for methods, see supplementary information). In addition, the body skin of starling nestlings from two separate populations (in Switzerland and Britain; see supplementary information) reflects in the ultraviolet (Fig. 1b,e), although the body skin of great-tit (Fig. 1d) and blackbird (*Turdus merula*) nestlings does not[6].

We investigated the function of this skin reflectance in starlings by applying ultraviolet-light blockers[8] on the nestlings' bodies and flanges and measuring their body-mass gain after two hours[9]. Nestlings with ultraviolet-reflecting skin ('+UV') gained relatively more mass than non-reflecting ('−UV') nestlings (difference in mass gain ± s.e.: +UV, 0.23 ± 0.14 g and −UV, -0.24 ± 0.12 g; $F_{1,27} = 4.84$, $P = 0.036$; when included as a random factor in the model (nest[random]), the nest effect was not significant, $F_{11,27} = 0.30$). In most broods, the mean mass gained by +UV nestlings was greater than that gained by −UV nestlings (sign test, $P = 0.038$). By contrast, we found that
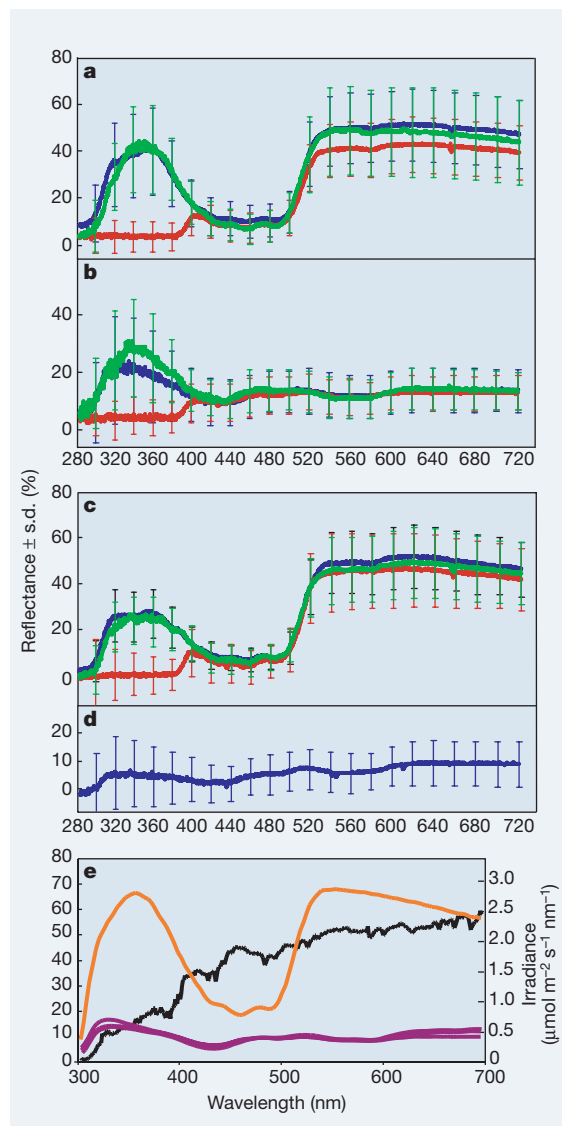
modifying ultraviolet reflectance on only the mouth flanges in both starling and great tit nestlings did not lead to significant differences in mass gain (starlings: $F_{1,101} = 0.38$, $P = 0.54$, nest[random] was not significant; great tits: $F_{2,330} = 0.142$, $P = 0.87$, nest[random] was not significant).

Our results indicate that artificial reduction of the ultraviolet reflectance of body skin and flanges affects mass gain by nestlings. The brightness of skin reflectance in ultraviolet and visible light by starling nestlings did not correlate with either their body mass or tarsus length, but showed a positive relation with their cell-mediated immune responses (see supplementary information; $F_{1,13} = 7.99$, $P = 0.014$; mean brood values: $F_{1,6} = 20.96$, $P = 0.006$). The

Figure 1 Reflectance spectra of nestling skin and nest irradiance. **a–d,** Reflectance spectra from nestling skin. Starlings: mouth flanges (**a**), *n* = 10; body skin (**b**), *n* = 10. Great tits: mouth flanges (**c**), *n* = 25; body skin (**d**), *n* = 22. Blue, untreated skin; red, skin treated with petroleum jelly containing ultraviolet-light blocker; green, skin treated with petroleum jelly without ultraviolet blocker; curves show medians ± s.d. **e,** Nest irradiance (black curve; *n* = 5) and reflectance spectra from mouth flanges (orange; *n* = 10) and body skin (purple; *n* = 6) of starling nestlings; median curves are shown.

brightness of nestling skin reflectance in these birds might therefore signal their phenotypic quality and/or condition[6,10].

An alternative explanation could be that nestlings that do not reflect in the ultraviolet might be less easily detected by their parents in dark nests (Fig. 1e) than those that do[9]. We found that ultraviolet-blocking material on the body skin spread after two hours to other young in the brood, reducing the overall body-skin ultraviolet reflectance of the brood. This reduction in ultraviolet contrast between the chicks and their nest, in association with differences in flange ultraviolet reflectance, could lead to less efficient chick detection by the parents, who rely on achromatic or chromatic mechanisms to detect them. This might explain the observed body-mass differences.

The phylogenetic patterns in the evolution of nano-structures[7] and the pigments responsible for ultraviolet reflectance by skin still need to be determined. Given the likely function of skin reflectance in parent–offspring communication, the ecological factors that affect skin reflectance and the associated parental responses should be investigated.

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