Do 'Quiet' Places Make Animals Placid? Island vs. Mainland Tiger Snakes

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Abstract

Most animals that possess potent venom display a wide variety of warning messages to discourage predators. Tiger snakes are large and highly venomous elapids that exhibit these anti-predator behaviours. We compared the anti-predator behaviours of two neighbouring and genetically indistinguishable populations in Western Australia (Herdsman Lake, HL and Carnac Island, CI). CI is free from human, native and feral predation. All of these factors represent a continual threat on HL situated on the mainland. Neither body size, nor sex influenced defensive behaviours. However, we observed a marked inter-population difference among adults in the degree to which anti-predator behaviours were displayed when snakes were continually aggravated: HL snakes exhibited a typical warning signal (flat-neck) and bite, while CI snakes remained very docile. In stark contrast, neonates of both populations exhibited marked anti-predator behaviours and both populations were indistinguishable in terms of the intensity of display. Neonates reared in captivity, hence regularly confronted by human predators, became more defensive in comparison with neonates exposed to natural conditions on CI; similarly several adult CI snakes kept in captivity became more defensive. Our results highlight the extreme behavioural plasticity of snakes. We also hypothesize that CI snakes may become more placid over time as they grow up in an environment free from predation.

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Introduction

Various alternative anti-predator tactics contribute to an animal's self-preservation, such as size, speed, fortification, crypsis, or aggressive displays. It is intuitive that distasteful, highly toxic species, or species that possess potent venom (i.e. snails, nudibranchs, insects, spiders, amphibians), should be advantaged if they can clearly advertise that they are dangerous or unpalatable (Goodale & Sneddon 1977; Brodie & Brodie 1980; Gittleman & Harvey 1980; Sillén-Tullberg 1990). Threatening colouration is often based on bands of contrasting colours (Smith 1975; Brodie & Janzen 1995), while anti-predator displays include raised postures, indicating willingness in some species to deliver their venom should a threat persist (Whitaker et al. 2000).

All of these anti-predator tactics serve as a warning to predators of the potential risk associated with the coveted prey and the same tactics have arisen independently many times across different lineages. Within squamate reptiles, venom has become highly derived and very toxic and almost all venomous snakes engage in an array of anti-predator repertoires to advertise their toxic disposition. In snakes, intimidation is a major and varied behavioural trait. Many species produce a loud hissing sound by blowing air through the glottis (e.g. *Bitis*), and make other noises to indicate their agitation, such as scraping their body scales against each other (*Cerastes*) or rattling their tail (*Crotalus*; Fenton & Licht 1990). Others have evolved bright and contrasted colours (*Micrurus*, *Elapsoide*; Brattstrom 1955; Jackson et al. 1976; Greene 1988; Brodie 1993a,b). The great majority of large species also raise a portion of their body off the ground and flatten the neck (Greene 1979; Rasmussen et al. 1995; Whitaker et al. 2000; Chippaux 2001). Intuition suggests that this makes them appear larger and more intimidating to a potential aggressor and warns of their willingness to strike. Widely recognized among 'Cobras' (e.g. *Naja*, *Ophiophagus*, *Hemachatus*, *Boulengerina*) and shield-nose snakes (*Aspidelaps*), this stance is also observed in highly venomous colubrids (e.g. *Dispholidus*, *Thelotornis*, *Toxicodryas*) and in many Australasian large elapids (e.g. *Notechis*, *Pseudechis*, *Pseudonaja*). As well as giving a warning signal when threatened, all of these species can bite and inject lethal doses of venom (Sutherland 1992; Chippaux 2001).

Besides the variety of anti-predator tactics used by different snake species, important geographic variations in behaviours have been documented among different populations of the same species (Burghardt 1971a; Arnold 1977; Ayres & Arnold 1983; Brodie & Garland 1993; Ford & Burghardt 1993; Burghardt & Schwartz 1999; Shine et al. 2003). Experience during development also influences the anti-predator behaviours of snake (Burghardt 1971b; Hampton & Gillingham 1989; Herzog 1990). Overall, anti-predator behaviours exhibited by snakes are likely to be the result of complex interactions between genetic and environmental factors (Brodie & Garland 1993; Burghardt & Schwartz 1999).

One of the assumptions for the evolution of anti-predator displays is that they should be more developed in ecological situations where the probability of predation or harassment is high (Coss 1999). In these scenarios there are strong

selective pressures favouring the evolution of such traits. In contrast, we may expect that the absence of predation will lead to a progressive reduction, either rapidly (phenotypic plasticity) or more slowly (through natural selection if exhibiting anti-predator behaviours is costly and hence possibly counter selected, or through genetic drift) of the expression of anti-predator behaviours. In this paper, we report data that support such a hypothesis. It should be noted that a lack of predators (hence the use of the term 'quiet place') does not necessarily mean a lack of stimulation in general; for instance, non-threatening species may well be detected without triggering an anti-predator response.

We took advantage of a contrasted ecological situation to examine the propensity of snakes to behave defensively when threatened: do snakes that live in a very quiet place, lacking predators, respond less to threatening situations than snakes that live in a much more hazardous place? We hypothesize that neonates (naïve snakes) will respond in an intermediate manner when compared with adults that experienced either hazardous or safe environments whilst growing. A complementary hypothesis is that anti-predator behaviour should respond over time to some degree (i.e. the intensity of defensive displays should increase with harassment) to changing environment.

Method

Study Species and Study Sites

Tiger snakes (*Notechis scutatus occidentalis [ater?]*) are large and highly venomous elapids (Broad et al. 1979; Cogger 1992). We compared the anti-predator behaviour of snakes belonging to two neighbouring populations in the south-west of Western Australia: Herdsman Lake (HL) (31°55′S; 115°48′E) and Carnac Island (CI) (32°07′S; 115°39′E). HL is a 300-ha perennial freshwater swamp Nature Reserve within the Perth metropolitan area. CI is a small island (also a nature reserve) situated 5 nautical miles off the coast of Perth. CI snakes may have been introduced to the island as little as 80 yr ago (Cann 1986; archives of Department of Conservation and Land Management in Western Australia). It is also possible that the population may be (partly?) composed of individuals that have immigrated from the mainland or nearby Garden Island (situated 1.1 nautical miles to the south) and/or have been marooned by the rising sea level 5000–7000 yr ago. Whatever the case, a virtual absence of divergence between CI and HL populations [< 0.3% in a matrix of genetic (five mitochondrial genes, 4825 bp) distances between CI and other Western Australia mainland, including HL, Tiger snakes; Scott et al. 2001; Keogh J.S., Scott I.A.W., Hayes, C. unpubl. data) makes them a suitable system for a comparative study of anti-predator behaviour.

Adult CI snakes have no natural or feral predators and do not suffer at all from human harassment. The presence of humans on CI is exceptional (category 'A' reserve with restricted access to the general public). In contrast, HL is an intensively managed recreation reserve utilized by the general public every day. The reserve is dissected by many pathways and boardwalks utilized by walkers,

cyclists and joggers, all of whom impact the tiger snake population either directly or indirectly. HL snakes also suffer predation from birds such as the swamp harrier (*Circus approximans*), Australian little eagle (*Hieraaetus morph-noides*) and the introduced kookaburra (*Dacelo gigas*), as well as cats and dogs (Ladyman M.T., pers. obs.).

The present investigation is based on results gathered from adults and neonates both in natural conditions and raised in captivity. This allows a greater range of comparisons (Arnold & Bennett 1984) than is possible from experiments conducted on neonates only (i.e. Mori & Burghardt 2000). Although the anti-predator behaviour of most snake species is logistically very difficult to study in the field (Shine et al. 2002), population density is very high in both sites (HL and CI; Bonnet et al. 1999, 2002; Aubret et al. 2004a) enabling behavioural observations on a reasonable number of individuals in standardized situations.

Anti-Predator Behaviours Displayed by the Snakes

Snakes generally attempt to flee when threatened (Whitaker & Shine 1999a; this study). However, individuals that are continually harassed (i.e. during manipulations) will embark on an impressive display of swaying and neck flattening that culminates in repeated strikes with an abundant release of venom. Components of this anti-predator display are easy to quantify (see below). These behaviours were progressive and typical of those normally observed in this species (Johnson 1975).

Experimental Design

In Nov. to Dec. 1999 and 2000 we collected data on 42 CI snakes and 32 HL snakes immediately in the field to ensure that snakes did not become accustomed to capture (Fitch 1975; Greene 1988). The snakes were located by sight whilst basking and were caught by hand. The time elapsed between snake location and the onset of the test was < 30 s. Investigations were conducted between 07:10 and 13:00 h. We chose to minimize disturbance to the snakes before behavioural tests (that lasted 3 min on average from capture to completion: see below); consequently we did not record body temperatures. However, complex effects of temperature on anti-predator tactics have been documented in snakes (Hertz et al. 1982; Arnold & Bennett 1984; Bennett 1984; Hailey & Davies 1986; Goode & Duvall 1989; Schieffelin & De Quieroz 1991; Keogh & DeSerto 1994; Passek & Gillingham 1997; Brodie & Russell 1999; Whitaker & Shine 1999a; Cooper 2000; Shine et al. 2000, 2002; Mori & Burghardt 2001; Webb et al. 2001). Hence, we were careful to conduct experiments only in moderate ambient temperatures (air temperature fluctuating between 15 and 25°C, usually 20°C) when tiger snakes are normally active and visible (during basking or foraging). Nevertheless, we do acknowledge a potential effect of difference in body temperature among the snakes tested. For instance, although snakes rapidly reach their preferred body temperature during basking and avoid overheating by ceasing basking (Peterson et al. 1993), it is possible that the later snakes tested were warmer because they

may have required less time to reach such preferred body temperature compared with the snakes caught earlier during the day. Importantly, the potential effect of various body temperatures on anti-predator behaviours was relatively equally distributed between CI and HL individuals as we collected the data over the same time period in the two study sites [on average at 8:50 h (7:10–11:00) on CI vs. 9.32 h (8:30–13:00) on HL. The difference between the two sites (ANOVA with the two sites as the factor and individual time at capture as the dependent variable; $p < 0.05$) is due to the fact that CI is a completely open (hence sunny) area compared with the relatively forested (hence more shady) HL area] and we therefore chose to collect data a little earlier on CI in an attempt to equalize snake temperatures in the two sites. This time-lag cannot explain our results, as all CI snakes were docile, while all HL snakes displayed marked anti-predator behaviours and very often flattened their neck (see results). Hence even the late CI snakes (presumably 'warm') remained docile, whereas even the early HL snakes (presumably 'cool') displayed vigorously.

Following experimental tests, we recorded sex, snout-vent length (SVL), and the body mass of each individual. Each individual was marked by scale clipping and then released (no individual is represented more than once in our data set). In every case, the first reaction of the snake to our presence was to try to escape. For our purposes it was thus necessary to place the snake in a critical situation to elicit anti-predator behaviours (Prior & Weatherhead 1994).

Experiment 1: Harassment in an Enclosure

Immediately after capture, each snake was placed in small portable enclosure that remained open at the top ($40 \times 36 \times 30$ cm, opaque walls). Within the enclosure a small shelter was made available, under which the tested individual could easily seek refuge ($22 \times 17 \times 6$ cm). When placed into the box, snakes had several alternatives: (i) to seek refuge, (ii) to remain immobile, (iii) to attempt escape, (iv) to display anti-predator behaviour (flattening of the neck and raising part of their body), (v) to try to strike at the observer, and (iv) or a combination of these. Each snake was left in the enclosure for 1 min with observers visible, but not intrusive (standing approx. 10 cm from the portable enclosure and as motionless as possible). Two observers were assigned to a specific role: one observer (always the same) handled the snakes whilst the other observer recorded the data. As the behaviour exhibited by the snakes was obvious and easy to quantify observers always agreed about behaviours exhibited. When individuals escaped they were immediately placed back in the enclosure.

For a further 30 s, snakes were placed under the shelter and were harassed by moving a stick 20 cm in front of the opening. The stick had a padded end making it an obvious target for the snake and allowing bites without injury. We recorded the number of strikes and bites delivered to the stick over the 30-s period (flat-neck displays were invisible). A snake under a 'safe' place (i.e. a shelter) will not try to escape or to bite unless the level of stress forces him to take major risks such as striking the aggressor and leaving the shelter. We interpreted escape attempt

and/or strikes as strong (i.e. desperate) reactions compared with the relative immobility of snakes that remained under the shelter.

Experiment 2: Harassment Whilst Restrained

The situation for the snakes was worsened. Immediately after expt 1 (thus, for each individual, expt 2 immediately followed expt 1), the same snakes were removed from the enclosure and were placed on the ground in an open area. They were gently immobilized by placing one foot lightly across the body, approximately one-third of the body length from the head. The pressure was moderate and the snake was able to move laterally and vertically, but was not able to escape restraint. Although harmless to the snake, such stimulus was intensive enough to elicit bites. As a further stimulus to provoke an anti-predator display we presented the snake whilst still underfoot with the stick consistently and continually over a 30-s period. As well as striking and biting the stick, other observed anti-predator behaviours included biting the boot under which they were restrained (in the analyses we pooled together bites on the boot and bites on the stick), flattening the head and raising the fore body off the ground.

No snakes were injured, and all individuals were immediately released at the exact place of capture. In the course of this study, the perturbation caused to the snakes was always brief, and many individuals (including the experimental snakes) were seen basking in the sun very close to the place of capture a few hours, to a few days, following the experiments. The Animal Ethics Committee of UWA approved all procedures (Project 01/100/177) and the Department of Conservation and Land Management (WA) issued fauna collection permits (permit #CE000347, SF003869).

Anti-Predator Behaviours of Neonates

To better identify the determinants (i.e. genetic factors in interaction with learning experience; Burghardt & Schwartz 1999) of anti-predator behaviours exhibited by two different populations we compared the anti-predator behaviours of naïve individuals: newborns. For this purpose, we captured 13 pregnant females (five from CI and eight from HL) that were kept in the laboratory until parturition in a controlled temperature room (27°C by day and 20°C by night). They were housed in individual cages (50 × 40 × 30 cm transparent plastic boxes) with water dish, shelter, and paper towel as substrate. A heat source provided basking opportunity four times a day (4 × 15 min/d, high pressure Na^+ lamp; 600 W). Water was available at all times and food offered approximately every 3 wk. We obtained 80 neonates (6 ± 5 per litter, $\bar{x}$ ± SD) for behavioural tests. Neonates were weighed soon after birth with an electronic scale (body mass; precision ± 0.1 g), measured in SVL and total length (precision ± 0.5 cm) and sexed by eversion of the hemipenes. They were housed in individual plastic boxes (20 × 10 × 5 cm) for the duration of the experiment, under the same conditions as the females. Tests were conducted no more than 12 h after birth. Each neonate

was restrained in the middle of the body using a stick wrapped with foam to prevent injury to the snake. We moved a pen (13 cm long and 2 cm of diameter, white in colour) towards the snake's head, trying to elicit a bite by moving the pen a few centimetres in front of it. The total number of bites elicited was scored for a 30-s period (the same time period as for the 'harassment whilst restrained' inflicted on adults in natural situations on CI and HL). We did not perform the whole series of tests on neonates so as to avoid excessive stress as neonates are sensitive and may become anorexic in captivity. However, we also counted the number of flat-neck displays after 3 mo of captivity at the completion of this experiment (see below). All behavioural tests on the neonates were carried out in the laboratory at 27°C; the average body temperature chosen by both HL and CI snakes in captivity is 26.8 ± 0.7°C (Ladyman & Bradshaw 2003).

Changes in Neonate Anti-Predator Behaviours over Time

We examined whether the snakes are able to modify their anti-predator behaviour over time and in response to different environments (Herzog & Burghardt 1986, 1988a; Herzog et al. 1989). Among the 80 neonates, 58 were kept in the laboratory in individual cages (food and water was provided) and tested 10 d, 1 and 3 mo after birth. The neonates were regularly manipulated for measurements, as such, they were disturbed several times a week. To evaluate the influence of captivity, we captured 10 neonates from unknown mothers at the CI site 3 mo after the parturition period and kept them in the laboratory for behavioural tests. It is unlikely that these 10 field-caught juveniles had previously encountered humans, and the absence of scars on their body suggests they had not been injured by any potential predator. As above, the total number of bites elicited over 30 s was scored, and behavioural tests were carried out in the laboratory at 27°C. All of these 10 young snakes came from CI, because 3-mo-old wild HL snakes escaped capture. We acknowledge that the lack of testing of such wild-caught young HL animals led to an incomplete design for this specific comparison (Herzog 1990). Nonetheless, results (see below) suggest that this did not invalidate entirely an assessment of the changes in neonatal anti-predator behaviours over time.

Does Captivity Influence the Anti-Predator Behaviours of Adults?

The anti-predator tactics adopted by adults may vary also in response to different situations. We recorded strike number as an index of the anti-predator attitude of adult CI and HL snakes caught in the field and kept in the laboratory, either in individual cages (under the same housing conditions as were the pregnant females) or in outdoor enclosures. Four HL, eight CI and another seven CI snakes were housed in three identical pits within the enclosures. Pits were 2 m in diameter and 1 m deep with sand substratum, and featured three large shelters (breeze blocks), a large water dish and one underground shelter. Hence, shade or cool were always available to the snakes. Direct sunlight provided basking opportunities for several hours a day. Captivity represented a radical change of

environment for all snakes with a smaller, defined space available and continual disturbance during husbandry procedures (on average the number of snake/human encounters was six per month, for events such as weighing etc.). Overall, 55 adult snakes (15 from CI and 40 from HL) were maintained in captivity for prolonged periods (128 ± 91 d in average). After at least 2 mo of captivity we recorded the number of strikes elicited in 30 s at an ambient temperature of 27°C. Prior to testing, each snake was removed from its external pit and maintained in the laboratory (situated 25 m away from the pits) in an individual cage (50 × 40 × 30 cm transparent plastic box with shelter, and paper towel as substrate) during 3 h; the snake was then placed on a carpet disposed on the floor. Each snake was tested as indicated in the expt 2 above.

Statistics

Some variables were normally distributed (i.e. SVL; all Shapiro–Wilk tests were non-significant) while others were not (i.e. wild adult CI snakes did not display any 'flat-neck' leading to a suite of null scores). Consequently, we used both parametric (ANOVA) and non-parametric tests (Mann–Whitney U-test, MWU-test). Our sample sizes were not always large, thus we used the adjusted z-score (Siegel 1956). Slight variations in sample size occurred, for instance because we decided to restrain the snake under the boot only after the eighth CI specimen tested. Although MWU-test is often considered as the most powerful (or sensitive) non-parametric alternative to the t-test for independent samples, we also used the Wald–Wolfowitz runs test to better assess the hypothesis that the two populations differ in some respect (i.e. not just with respect to the mean, but also with respect to the general shape of the distribution). When using MWU or Wald–Wolfowitz runs tests led to similar results only the former were presented. For the analyses based on the neonates kept in captivity, we used a mixed model ANOVA procedure with the mother as a random factor to take into account possible maternal pseudo-replication effects on neonates' behaviour. Changes in anti-predator behaviours over time on the same individuals (captive neonates) were analysed through repeated measures analyses of variance with snake's origin (CI or HL) as between-subjects factors and the number of strikes as the dependent variable (Greenhouse & Geisser 1959; O'Brien & Kaiser 1985; Forsman 1996). Mean values are presented with their standard deviation; p-values were two-tailed. Statistics were carried out with Statistica 6.0 software (Statsoft 2000, Tulsa, OK, USA; http://www.statsoft.com).

Results

Body Size: Comparisons between the Two Populations

Body size of all snakes tested is given in the Table 1. On average, CI snakes were larger than HL ones (ANOVA with provenance as the factor and SVL as the dependent variable: $F_{1,72} = 33.3$, p < 0.00001) and heavier when the effect of size was taken into account (ANCOVA with SVL as a covariate: $F_{1,69} = 11.34$, p = 0.001;

Table 1: Body sizes (snout-vent length, SVL) and body condition (body mass adjusted to body size: using body mass as a dependent variable and SVL as a covariate in ANCOVAS) of adult (females vs. males) and neonate tiger snakes from Carnac Island and Herdsman Lake

Population	Sex (N)	Snout vent length (cm)	Adjusted body mass (g)
Adults			
Carnac	Females (13)	80.2 ± 5.1 (72.0–88.5)	337.6 ± 21.3
Carnac	Males (29)	93.5 ± 10.6 (65.5–105.0)	382.3 ± 15.3
Herdsman	Females (16)	71.7 ± 5.7 (60.5–79.0)	279.4 ± 20.2
Herdsman	Males (16)	80.6 ± 6.9 (65.5–90.0)	325.9 ± 20.0
Neonates			
Carnac	32	20.4 ± 1.2 (17.5–22.5)	5.78 ± 0.63
Herdsman	48	17.15 ± 1.2 (14.0–19.5)	5.27 ± 0.70

Values are expressed as $\bar{x} \pm SD$, followed by the range.

Table 1). Males attained larger body size than females from the same populations, but there was no difference in the degree of sex dimorphism between the two populations (two-factor ANOVA with provenance and sex as the factors, and SVL as the dependent variable; effect of provenance: $F_{1,70} = 29.1$, p < 0.00001; effect of sex: $F_{1,70} = 31.4$, p < 0.00001; interaction: $F_{1,70} = 1.3$, p $= 0.26$).

Influence of Body Size and Sex on Anti-Predator Behaviours

Despite the size difference between HL and CI snakes, the size of both females and males of the two populations largely overlapped; hence it was possible to compare CI snakes and HL snakes in a straightforward way. A generalized mixed model ANOVA with behaviour as the dependent variable, sex (fixed factor), SVL (covariate) and population (CI vs. HL as a random factor) failed to detect any effect of sex or SVL (all p > 0.40) without interaction between them (all p > 0.05). When sex and population were considered separately, we found no effect of body size or sex on the anti-predator traits we observed (all ANOVA with sex as the factor, correlation with size as the independent variable, or ANCOVA to take both into account, gave p-values > 0.05; Fig. 1). The correlations between these variables were almost always positive however, suggesting that if a larger sample had been used, we may have found a positive influence of size on anti-predator behaviour. The mean sample size required to have obtained a 'significant' effect (with $\alpha < 0.05$ and $\beta < 0.1$) was 324 ± 359 (range 31–1046, N = 8 correlation analyses), suggesting that the effect of body size, if any, was probably slight.

Anti-Predator Behaviour When the 'predator' is Close to the Snake

When snakes were placed into the box and observed, but not disturbed (Fig. 2), HL snakes spent more time in the open than did CI snakes which hid under the shelter more often [MWU-test: adjusted $Z = -3.88$, N = 42 and 32, p < 0.0001; Fig. 2a]. HL individuals also attempted to escape more frequently than CI snakes, despite our obvious presence (4.1 ± 3.2 vs. 1.1 ± 1.7; MWU-test: adjusted
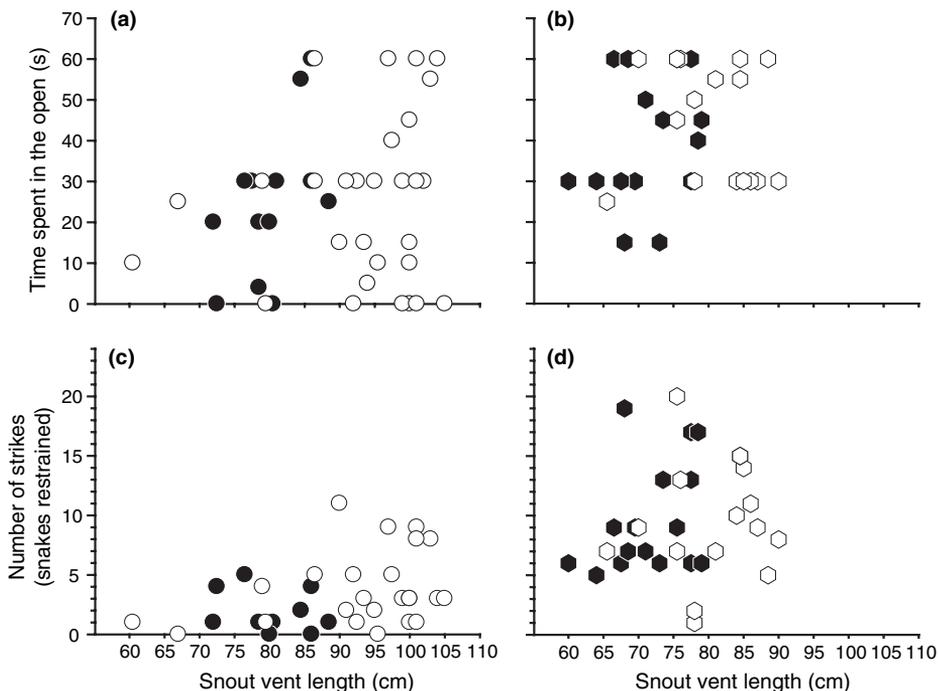
Fig. 1: Body size does not influence the time that confined snakes spent exposed in a portable enclosure fitted with a small shelter (a, b: values equal to zero mean that the snake hid itself immediately), nor does it influence the number of strikes delivered towards the observer whilst snakes were restrained underfoot (c, d). This relationship was consistent when data were pooled or when sex (black symbols represent females, open symbols represent males) and population (circles represent Carnac Island snakes; hexagons represent Herdsman lake snakes) were considered separately. Black circles = females from Carnac Island; open circles = males from Carnac Island; black hexagons = females from Herdsman Lake; open hexagons = males from Herdsman Lake

$Z = -4.37$, N = 42 and 32, p < 0.0001; Fig. 2b). HL snakes struck spontaneously more often than CI snakes (MWU-test: adjusted $Z = -2.08$, N = 42 and 32, p = 0.038; Fig. 2c). Seventy one per cent of HL snakes also displayed a flattened neck but CI snakes never showed flattened neck during the tests (MWU-test performed using a score for each individual, not percentages: adjusted $Z = -6.43$, N = 42 and 32, p < 0.0001; Fig. 2d). Using the frequency of display per unit time out of the shelter, as flat neck displays were invisible when snakes were under the shelter, did not change the result as CI snakes never displayed with a flattened neck.

Anti-Predator Behaviour When the Snake is Under Shelter and Harassed

When placed under the cover of the small shelter in the box (Fig. 3a), all snakes tended to remain sheltered. However, HL snakes were more prone to bite the stick moving in front of them (MWU-test: adjusted $Z = -4.82$, N = 41 and 29, p < 0.0001); and, despite their relatively smaller size (providing more room in
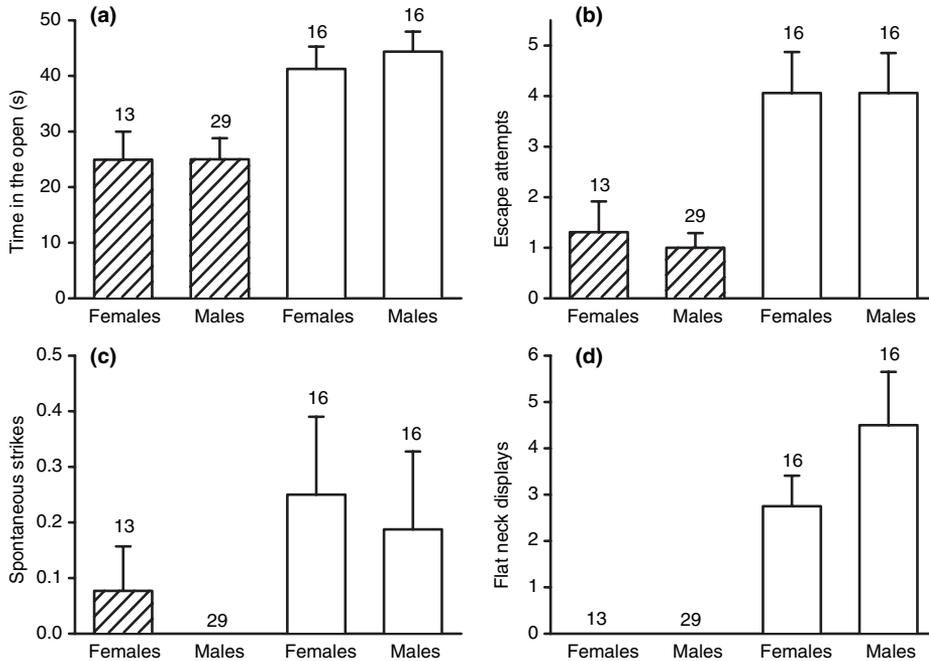
Fig. 2: Tiger snakes from Carnac Island (CI, hatched bars) and Herdsman Lake (open bars) exhibit very different anti-predator behaviours. The four graphs represent the frequency that each response type was selected in individuals from both populations. CI snakes sort refuge under the shelter more often (a); attempted escape less often (b); rarely struck at observers (c, note the scale on the y axis); and they did not flatten their neck (d). Data are expressed as $\bar{x} \pm$ SE; the numbers indicate sample size

the shelter), they came out of the shelter more often when compared with CI snakes [only one CI snake (2%) came out of the shelter vs. 17 HL snakes (59%); MWU-test: adjusted $Z = -5.18$, N = 41 and 29, p < 0.0001].

Anti-Predator Behaviour When Snakes are Restrained

When restrained under the boot (Figs 3b and 4), HL snakes bit the boot and the stick they were harassed with more often than CI snakes (MWU-test: adjusted $Z = -5.40$, N = 34 and 32, p < 0.0001). Similarly, they often displayed a flattened neck whilst CI snakes did not (MWU-test: adjusted $Z = -2.49$, N = 25 and 22, p = 0.01; Fig. 4).

Anti-Predator Behaviour of Neonates

Compared with HL snakes, CI neonates were larger (mixed model ANOVAS with maternal identity as a random factor to take into account maternal effect and neonate SVL as the dependent variable; $F_{1,11} = 15.27$, p < 0.0001) but were not in better body condition (same design mixed model ANCOVA with neonate SVL as
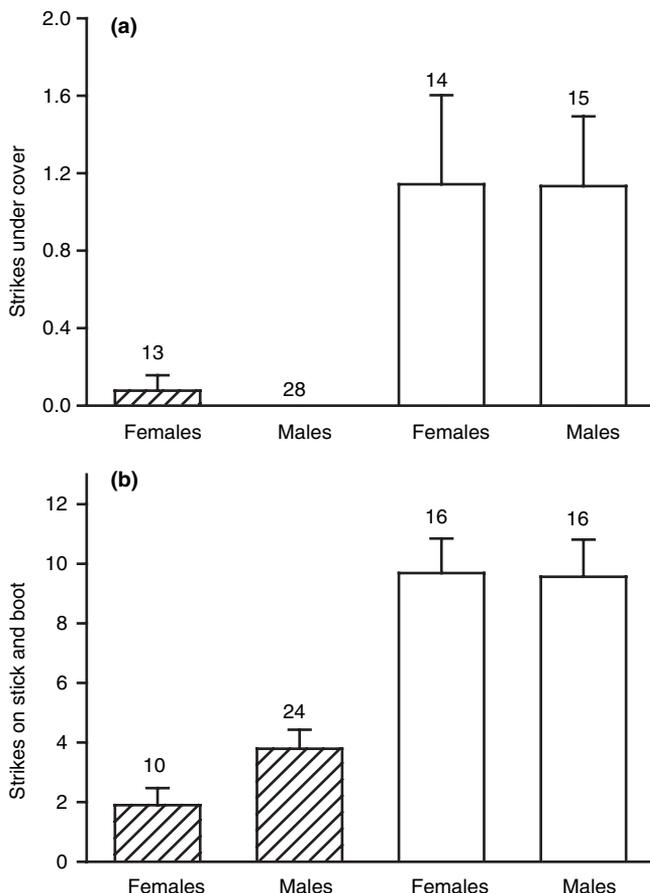
Fig. 3: When snakes were placed under the shelter and harassed with a stick moved continuously in front of them for 30 s, Carnac Island (CI) snakes very rarely struck or bit the stick, compared with Herdsman Lake (HL) snakes (a); similarly, when restrained under foot and harassed for 30 s, anti-predator behaviours (bites on the stick and on the boot pooled) were less frequent than in HL snakes (b). CI snakes are represented by hatched bars while HL snakes are represented by open bars. Data are expressed as x̄ ± SE; the numbers indicate sample size

a covariate and neonate body mass as the dependent variable; $F_{1,11} = 3.02$, p = 0.11; Table 1). However, neonates from both sites did not differ in the number of strikes elicited by harassment (mixed model ANOVA: $F_{1,10} = 0.20$, p = 0.67; Fig. 5). Neonates responded intensively to harassment with a high number of strikes towards the aggressor compared with adults (Fig. 5).

Changes over Time in the Anti-Predator Behaviour of Neonates

From birth to 3 mo of age, the young snakes tended to respond more intensively (repeated measures over time: Wilks $\lambda = 0.714$, $F_{4,53} = 5.30$, p =
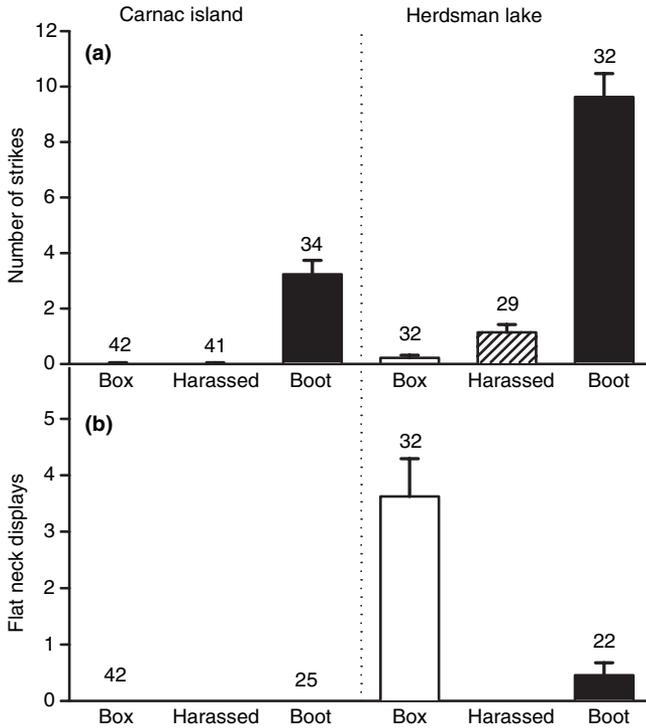
Fig. 4: Anti-predator behaviours were increasingly frequent as the threat to the snakes increased (a). The threat to snakes increased as each was placed in the portable enclosure (= box), harassed with a stick when under shelter, and finally restrained underfoot. Notably the number of spontaneous strikes was very low, but many snakes bit repeatedly when kept under foot and harassed. As the number of bites increased, the number of threatening displays (flat neck) decreased (b). Note that flat neck displays remained invisible to the observer when the snakes were under the shelter. Data are expressed as $\bar{x} \pm$ SE; the numbers indicate sample size

0.001; specific effect of time: $F_{3,168} = 8.65$, p < 0.0001; Fig. 5). Although the exact trajectory exhibited by CI and HL neonates over the 3 mo of experiment differed, with a regular and progressive increase in CI neonates and a more irregular increase for HL snakes (interaction between time and origin of the snake: $F_{3,168} = 3.84$, p = 0.01); the overall anti-predator behaviour of CI snakes was not less intense compared with HL snakes, a weak reverse trend being observed instead (effect of snake origin: $F_{1,56} = 4.46$, p = 0.04; Fig. 5). A mixed model ANOVA with maternal identity as a random factor to take into account maternal effect and neonate anti-predator behaviour as the dependent variable suggested that the HL and CI snakes responded with the same intensity after 3 mo of captivity in terms of number of defensive strikes ($F_{1,6} = 0.88$, p = 0.39). Similarly, flat-neck displays were observed in the same proportion among HL and CI snakes (38.7% HL vs. 23.1% CI snakes flattened their neck; $\chi^2 = 1.60$, df = 1, p = 0.21). In stark contrast, the 3-mo-old CI snakes caught in the field (N = 10) were very placid compared to the same-age snakes maintained in captivity and
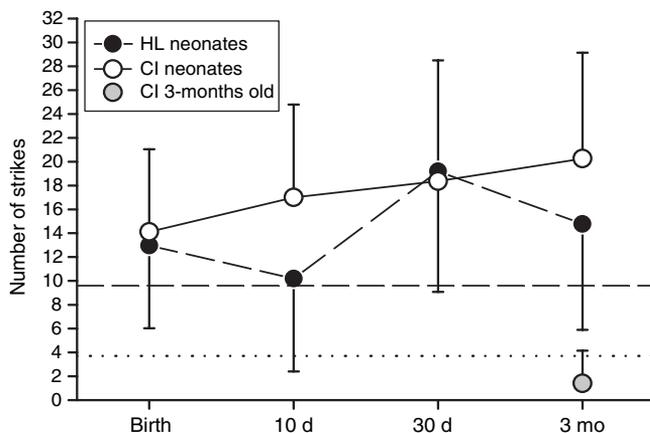
Fig. 5: Neonates from Carnac Island (CI, open circles) and from Herdsman Lake (HL, black circles) responded with similar intensity (number of strikes) when harassed (see text). In captivity tiger snakes tended to respond more intensively at 3 mo of age than at birth. In strong contrast, same-age snakes caught in the field (grey circle) were very docile. The two lines provide the average value observed in adults, from HL (dashed) and CI (dotted) respectively. Each symbol represents a mean value along with the standard deviation

were reluctant to strike [mixed model ANOVA with mother identity as a random factor and snake provenance (laboratory vs. wild) as the fixed factor: $F_{1,16} = 18.81$, p < 0.001; Fig. 5]. Only one 3-mo-old wild snake among 10 flattened its neck, while 32% of the captive snakes did ($\chi^2 = 1.95$, df = 1, p = 0.16).

Effect of Captivity on Adults

The CI adult snakes maintained in captivity were larger compared with HL snakes (mean SVLs were respectively 84.8 ± 6.35 and 76.7 ± 6.32 cm; $F_{1,53} = 17.83$, p = 0.0001). The number of strikes observed in snakes kept in the laboratory in individual cages did not differ from the number recorded in snakes kept in outdoor enclosures (8.08 ± 8.30 vs. 5.63 ± 6.57 respectively, $F_{1,53} = 1.24$, p = 0.270). The number of strikes elicited in response to harassment was greater in HL snakes compared with CI snakes (8.13 ± 8.16 vs. 4.87 ± 6.29 respectively) but this difference did not reach statistical significance ($F_{1,53} = 1.95$, p = 0.168). Comparison with the results gathered in the field suggest that after a prolonged period of captivity, CI snakes tended to increase the intensity of their anti-predator behaviours while HL snakes showed a decrease (comparing number of defensive strikes recorded in the field vs. in captivity: Wald-Wolfowitz runs test z-adjusted = 2.84, p < 0.005 for CI snakes; Wald-Wolfowitz runs test z-adjusted = 1.22, p = 0.18 for HL snakes); in addition the variance increased in both groups. Notably, although seven captive CI adults among the 15 tested remained very placid (no strike), five (33%) became very defensive and delivered 11–16 strikes. In comparison, only one CI snake (3%) struck 11 times (the maximum observed) among the 34 individuals tested in the field. Only one HL

snake (3%) among the 32 tested in the field did not strike; but 11 (28%) among the 40 tested in captivity refused to strike.

Discussion

Our data reveal that even small degrees of spatial separation (< 25 km) can lead to a marked divergence in the intensity of the anti-predator behaviours – from placidity to vigorous defence – exhibited by adults from two separate populations of tiger snakes. Two alternative and non-exclusive hypotheses may explain such divergence. First, a genetic difference may exist in the mechanisms that control the intensity of anti-predator behaviours, for example CI snakes may have lost the ability to flatten their neck (Arnold 1980; Mori & Burghardt 2000). Secondly, phenotypic flexibility influenced by environmental conditioning may exist in these same mechanisms (Burger 1989, 1990; Alcock 1993; Webb et al. 2001). During the current investigation, and despite strong divergence in the intensity of the anti-predatory defences, we observed strong similarities between mainland and island populations. Notably, we observed the same anti-predator repertoire in CI and HL snakes, from the systematic tendency to attempt escape prior to initial capture, to anti-predator displays after a sufficient threat was inflicted. Although the flat-neck display was not recorded in the field in CI snakes in the present investigation, we observed it on later occasions in the field (2%, N = 208 captures) and in captivity. Overall, our results revealed very strong inter-population and age-class differences in the degree of the expression of anti-predator behaviours, rather than clear-cut differences in the anti-predator repertoire.

Flight responses often take precedence over all other activities (Dixon 1998). It is therefore not surprising that this was a shared response between CI and HL populations (Whitaker & Shine 1999a). Only when animals were faced with inescapable threats, did they revert to anti-predator strategies (Greene 1988; Prior & Weatherhead 1994). The results gathered on HL snakes and on all neonates were also not surprising. The majority of individuals displayed warning signals before striking and biting behaviours commenced: as the intensity of our threat increased, the anti-predator response intensified (Arnold & Bennett 1984; Prior & Weatherhead 1994; Whitaker et al. 2000; Shine et al. 2002). Most striking, however, was the contrasted response of CI tiger snakes that were extremely placid. This is counterintuitive to what was expected of a large and venomous animal. On CI, snakes (at least the adults) have no natural or feral predators. Therefore, the CI snakes have little cause to become defensive (Maddox 1993; Kitchener 1996; Coss 1999). Alternatively, diseases or parasite load may cause drowsiness and result in the observed docility of CI snakes. The body condition of a snake is an accurate indicator of its foraging success (Bonnet et al. 2001; Lourdais et al. 2002), and sick snakes are anorexic. However, CI snakes were in better condition than HL, making it unlikely that the population differences in behaviour were due to weakness or illness in the CI snakes. In addition, although HL snakes carry significant parasite loads, CI snakes are virtually parasite-free, probably due to the absence of secondary hosts on the waterless island (Bonnet

X., pers. obs.). Another explanation for this docility may be that CI snakes have become habituated to mild agitation, such as the continuous stimulus of the thousands of seabirds that inhabit the island; such agitation may raise the threshold above which anti-predator attacks are launched through habituation (Herzog et al. 1989). In stark contrast, snakes inhabiting HL are confronted by many threatening situations (e.g. raptors, kookaburra, cats, dogs, etc.) mostly caused by humans (HL is crossed by many pathways and regularly managed, the basking zones being mown). Human/snake encounters often result in the snake being injured or killed (Herzog & Burghardt 1988b; Whitaker & Shine 1999a; Whitaker 1999). Perhaps snakes accurately adjust their anti-predator behaviours to the degree of threat they experience, or to other characteristics of their habitat, such as quality and availability of shelters (i.e. the thick and dark bushes that cover CI provide safe harbours; Dickman 1992). If this hypothesis is valid we may expect that either neonates and/or adults are able to rapidly modify the intensity of their anti-predator attitude when confronted with different environments. Data gathered during the captivity experiments support this notion.

As generally observed in snakes (Arnold & Bennett 1984), neonates from both populations exhibited intensive anti-predator behaviours with an increase in such intensity over time in captivity. However, young snakes (3-mo old) caught in the field on CI were remarkably docile compared with snakes of the same age held in captivity. We do not know if the snakes that were born on CI became docile or were already very quiet at birth. Indeed, the mothers of the captive neonates were caught before parturition and may have been stressed and somehow influenced (i.e. through hormonal cues) the behaviour of their offspring during pregnancy. The influence of maternal (or incubation) environment on neonate behaviour and mobility has been documented in different taxa (Burghardt 1970; Burger 1989, 1990, 1991, 1998; Bernardo 1991, 1996; Sorci & Clobert 1997; Sood et al. 2001; Webb et al. 2001). Whatever the case, our results show that changing environmental conditions (either intrauterine or after birth) led to marked differences in anti-predator behaviour. This also applies to adult tiger snakes maintained in captivity. CI and HL snakes tended to respond the same way when they were kept under similar environment. Our results suggest that some of the very placid adult CI snakes became more defensive in response to previously unencountered harassment while some of the very defensive HL became more placid, possibly due to habituation.

The strong similarities between CI and HL neonates and a virtual lack of genetic variance between the two populations suggest that our results probably reflect nurtured differences. However, because genetic studies sample only a very small fraction of the genome, lack of difference for the fractions sampled cannot be used to argue that there is no difference in the specific genetic basis of the anti-predatory defences. It remains possible that selection has acted on the behavioural response to threat (Garland 1988) and we do not claim any certainty in the proximate mechanisms involved in the population divergences.

Although our study is based on two populations only, our captive experiments show that the anti-predator behaviour of tiger snakes is flexible, as

documented in other snake species (Herzog & Burghardt 1986, 1988a; Burger 1989, 1990; Herzog et al. 1989; Webb et al. 2001). In addition, such flexibility was expressed as expected within the CI/HL context: placid tiger snakes inhabit a relatively quiet place whilst very responsive tiger snakes live in a more hazardous place, and such tendency is experimentally partly reversible. The CI/HL system provides an exceptional opportunity to examine the adaptive value of phenotypic plasticity in anti-predator behaviours vs. the adaptive value of a selected behavioural trait (Aubret et al. 2004b). More generally, tiger snakes have colonized very diverse habitats, both on the mainland and on islands (Schwaner 1991). Such diversity in the habitats is probably associated with divergence in predation threat (i.e. many islands lack predators for tiger snakes). In the future, it would be interesting to better assess the respective influence of possible genetic divergences (although the two neighbouring populations, CI vs. HL, were genetically indistinguishable, they may diverge in un-sampled alleles involved in anti-predator behaviour) and of phenotypic plasticity on the anti-predator behaviours of tiger snakes. This will allow us to assess more fully the longstanding (i.e. Darwin 1845 already suggested that islands may well have a tameness effect on animals) and largely admitted (Stamps & Buechner 1985; Shine et al. 2002), yet untested, hypothesis that quiet places make animals placid.

Acknowledgements

Literature Cited

Alcock, J. 1993: The development of behavior. In: Animal Behavior: an Evolutionary Approach, 5th edn (Farley, P., ed.). Sinauer Associates Inc, Sunderland, MA, pp. 89—116.

Arnold, S. J. 1977: Polymorphism and geographic variation in feeding behaviour of garter snakes *Thamnophis elegans*. Science **197,** 676—678.

Arnold, S. J. 1980: The microevolution of feeding behavior. In: Foraging Behavior: Ecological, Ethological and Psychological Approaches (Kamil, A. & Sargent, T., eds). Garland STPM press, New York, pp. 409—453.

Arnold, S. J. & Bennett, A. F. 1984: Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. Anim. Behav. **32,** 1108—1118.

Aubret, F., Bonnet, X., Maumelat, S., Bradshaw, S. D. & Schwaner, T. 2004a: 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. 2004b: Adaptive developmental plasticity in snakes. Nature **431,** 261—262.

Ayres, F. A. & Arnold, S. J. 1983: Behavioural variation in natural populations. IV. Mendelian models and heritability of a feeding response in the garter snake, *Thamnophis elegans*. Heredity **51,** 405—413.

Bennett, A. F. 1984: Thermal dependence of muscle function. Am. J. Physiol. **247,** 217—229.

Bernardo, J. 1991: Manipulating egg size to study maternal effects on offspring traits. Trends Ecol. Evol. **6,** 36—37.

Bernardo, J. 1996: Maternal effects in animal ecology. Am. Zool. **36,** 83—105.

Bonnet, X., Bradshaw, S. D., Shine, R. & Pearson, D. 1999: Why do snakes have eyes? The (non-) effect of blindness in island tiger snakes. Behav. Ecol. Sociobiol. **46,** 267—272.

Bonnet, X., Naulleau, G., Shine, R. & Lourdais, O. 2001: Short-term versus long-term effects of food intake on reproductive output in a viviparous snake (*Vipera aspis*). Oikos **92,** 297—308.

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. Aust. Ecol. **27,** 442—450.

Brattstrom, B. H. 1955: The coral snake 'mimic' problem and protective coloration. Evolution **9,** 217—219.

Broad, A. J., Sutherland, S. K. & Coulter, A. R. 1979: The lethality in mice of dangerous Australian and other snake venom. Toxicon **17,** 661—664.

Brodie, E. D., III. 1993a: Consistency of individual differences in antipredator behaviour and colour pattern in the garter snake *Thamnophis ordinoides*. Anim. Behav. **45,** 851—861.

Brodie, E. D., III. 1993b: Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution **47,** 227—235.

Brodie, E. D. Jr. & Brodie, E. D., III 1980: Differential avoidance of mimetic salamanders by free-ranging birds. Science **208,** 181—183.

Brodie, E. D., III. & Garland, T. Jr. 1993: Quantitative genetics of snake populations. In: Snakes: Ecology and Behavior (Seigel, R. A. & Collins, J. T., eds). McGraw-Hill, New York, pp. 315—362.

Brodie, E. D., III. & Janzen, F. J. 1995: Experimental studies of coral snake mimicry: generalised avoidance of ringed snake patterns by free-ranging avian predators. Funct. Ecol. **9,** 186—190.

Brodie, E. D. I. & Russell, N. H. 1999: The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes. Anim. Behav. **57,** 445—451.

Burger, J. 1989: Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). Behav. Ecol. Sociobiol. **24,** 201—207.

Burger, J. 1990: Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*) and kingsnakes (*Lampropeltis getulus*). J. Herpetol. **24,** 158—163.

Burger, J. 1991: Effects of incubation temperature on behavior of hatchling pine snakes: implications for reptilian distribution. Behav. Ecol. Sociobiol. **28,** 297—303.

Burger, J. 1998: Effects of incubation temperature on behavior of hatchling pine snakes: implications for survival. Behav. Ecol. Sociobiol. **43,** 11—18.

Burghardt, G. M. 1970: Chemical-cue preferences of newborn garter snakes: influence of prenatal maternal experience. Science **171,** 921—923.

Burghardt, G. M. 1971a: Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (*Thamnophis sirtalis*). Behaviour **36,** 246—257.

Burghardt, G. M. 1971b: Learning processes in reptiles. In: Biology of the Reptilia, Vol. 7 (Gans, C. & Tinkle, D., eds). Academic, New York, pp. 555—681.

Burghardt, G. M. & Schwartz, J. M. 1999: Geographic variations on methodological themes in comparative ethology: a natricine snake perspective. In: Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms (Foster, S. A. & Endler, J. A., eds). Oxford Univ. Press, Oxford, pp. 69—94.

Cann, J. 1986: Snakes Alive. Kangaroo Press, Sydney.

Chippaux, J. P. 2001: Les serpents d'Afrique occidentale et centrale. Institut de Recherche pour le Développement, Paris.

Cogger, H. G. 1992: Reptiles and Amphibians of Australia. Reed Books, Cornell Univ. Press, Chastwood, NSW.

Cooper, W. E. Jr. 2000: Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). Behaviour **137,** 1299—1315.

Coss, R. G. 1999: Effects of relaxed natural selection on the evolution of behavior. In: Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms (Foster, S. A. & Endler, J. A., eds). Oxford Univ. Press, Oxford, pp. 180—208.

Darwin, C. 1845: Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, 2nd edn. John Murray, London.

Dickman, C. R. 1992: Predation and habitat shift in the house mouse *Mus domesticus*. Ecology **73,** 313—322.

Dixon, A. K. 1998: Ethological strategies for defence in animals and humans: their role in some psychiatric disorders. Br. J. Med. Psychol. **71,** 417—445.

Fenton, M. B. & Licht, L. E. 1990: Why rattle snake? J. Herpetol. **24,** 274—279.

Fitch, H. S. 1975: A Demographic Study of the Ringneck Snake (*Diadophis punctatus*) in Kansas. University of Kansas Museum of Natural History, Miscellaneous Publications **62,** 1—53.

Ford, N. B. & Burghardt, G. M. 1993: Perceptual mechanisms and the behavioural ecology of snakes. In: Snakes: Ecology and Behavior (Seigel, R. A. & Collins, J. T., eds). McGraw-Hill, New York, pp. 117—164.

Forsman, A. 1996: An experimental test for food effects on head size allometry in juvenile snakes. Evolution **50,** 2536—2542.

Garland, T. 1988: Genetic basis of activity metabolism. I. Inheritance of speed, stamina and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution **42,** 335—350.

Gittleman, J. L. & Harvey, P. H. 1980: Why are distasteful prey not cryptic? Nature **286,** 149—150.

Goodale, M. A. & Sneddon, I. 1977: The effect of distastefulness of the model on the predation of artificial Batesian mimics. Anim. Behav. **25,** 660—665.

Goode, M. J. & Duvall, D. 1989: Body temperature and defensive behaviour of free-ranging prairie rattlesnakes, *Crotalus viridis viridis*. Anim. Behav. **38,** 360—362.

Greene, H. W. 1979: Behavioral convergence in the defensive displays of snakes. Experientia **35,** 747—748.

Greene, H. W. 1988: Antipredator mechanisms in reptiles. In: Biology of the Reptilia, Vol. 16 (Gans, C. & Huey, R. B., eds). Alan Riss, New York, pp. 1—52.

Greenhouse, S. W. & Geisser, S. 1959: On methods in the analysis of profile data. Psychometrika **24,** 95—112.

Hailey, A. & Davies, P. M. C. 1986: Effects of size, sex, temperature and condition on activity metabolism and defense behaviour of the viperine snake, *Natrix maura*. J. Zool. **208,** 541—558.

Hampton, R. E. & Gillingham, J. C. 1989: Habituation of the alarm reaction in neonatal eastern garter snakes, *Thamnophis sirtalis*. J. Herpetol. **23,** 433—435.

Hertz, P., Huey, R. B. & Nevo, B. 1982: Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. **30,** 676—679.

Herzog, H. A. Jr 1990: Experimental modification of defensive behaviors in garter snakes *Thamnophis sirtalis*. J. Comp. Psychol. **104,** 334—339.

Herzog, H. A. Jr & Burghardt, G. M. 1986: Development of antipredator responses in snakes: I. Defensive and open-field behaviors in newborns and adults of three species of garter snakes (*Thamnophis melanogaster*, *T. sirtalis*, *T. butleri*). J. Comp. Psychol. **100,** 372—379.

Herzog, H. A. Jr. & Burghardt, G. M. 1988a: Development of antipredator responses in snakes: III. Stability of individual and litter differences over the first year of life. Ethology **77,** 250—258.

Herzog, H. A. Jr. & Burghardt, G. M. 1988b: Attitudes towards animals: origins and diversity. Antrozoös **1,** 214—222.

Herzog, H. A. Jr, Bailey Bowers, B. & Burghardt, G. M. 1989: Development of antipredator responses in snakes: IV. Interspecific and intraspecific differences in habituation of defensive behavior. Dev. Psychobiol. **22,** 489—508.

Jackson, J. F., Ingram, W. & Campbell, H. W. 1976: The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. Am. Nat. **110,** 1029—1053.

Johnson, C. R. 1975: Defensive display behaviour in some Australian and Papuan-New Guinean pygopodid lizards, boid, colubrid and elapid snakes. Zool. J. Linn. Soc. **56,** 265—282.

Keogh, J. S. & DeSerto, F. P. 1994: Temperature dependent defensive behavior in three species of North American colubrid snakes. J. Herpetol. **28,** 258—261.

Kitchener, A. 1996: Justice at last for the dodo. New Sci. **1888,** 24—27.

Ladyman, M. & Bradshaw, D. 2003: The influence of dehydration on the thermal preferences of the Western tiger snake, *Notechis scutatus*. J. Comp. Physiol. B, **173,** 239—246.

Lourdais, O., Bonnet, X. & Doughty, P. 2002: Costs of anorexia during pregnancy in a viviparous snake (*Vipera aspis*). J. Exp. Zool. **292,** 487—493.

Maddox, J. 1993: Bringing extinct dodo back to life. Nature **365,** 291.

Mori, A. & Burghardt, G. M. 2000: Does prey matter? Geographic variation in antipredator responses of hatchling natricine snakes, *Rhabdophis tigrinus tigrinus*, a snake with nuchal glands. Ethology **107,** 795—811.

Mori, A. & Burghardt, G. M. 2001: Thermal effects on antipredator behavior of *Rhabdophis tigrinus* hatchling natricine snakes. J Comp Psychol **114,** 408—413.

O'Brien, R. G. & Kaiser, M. K. 1985: MANOVA method for analysing repeated measures designs: an extensive primer. Psychol. Bull. **97,** 316—333.

Passek, K. M. & Gillingham, J. G. 1997: Thermal influence on defensive behaviours of the Eastern garter snake, *Thamnophis sirtalis*. Anim. Behav. **54,** 629—633.

Peterson, C. R., Gibson, A. R. & Dorcas, M. E. 1993: Snake thermal ecology: the causes and consequences of body-temperature variations. In: Snakes: Ecology and Behavior (Seigel, R. A. & Collins, J. T., eds). McGraw-Hill, Inc., New York, pp. 241—314.

Prior, K. A. & Weatherhead, P. J. 1994: Response of free-ranging eastern massasauga rattlesnakes to human disturbance. J. Herpetol. **28,** 255—257.

Rasmussen, S., Young, B. & Krimm, H. 1995: On the 'spitting' behaviour in cobras (Serpentes: Elapidae). J. Zool. **237,** 27—35.

Schieffelin, C. D. & De Quieroz, A. 1991: Temperature and defense in the common garter snake: warm snakes are more aggressive than cold snakes. Herpetologica **47,** 230—237.

Schwaner, T. D. 1991: Spatial patterns in tiger snakes (*Notechis ater*) on offshore islands of southern Australia. J. Herpetol. **25,** 278—283.

Scott, I. A. W., Hayes, C., Keogh, J. S. & Webb, J. K. 2001: Isolation and characterization of novel microsatellite markers from the Australian tiger snakes (Elapidae: *Notechis*) and amplification in the closely related genus *Hoplocephalus*. Mol. Ecol. Notes **1,** 117—120.

Shine, R., Olsson, M., Lemaster, M. P., Moore, I. T. & Mason, R. T. 2000: Effects of sex, body size, temperature, and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Coluridae). Behav. Ecol. **11,** 239—245.

Shine, R., Sun, L. X., Fitzgerald, M. & Kearney, M. 2002: Antipredator responses of free ranging pit vipers (*Gloydius shedaoensis*, Viperidae). Copeia **2002,** 843—850.

Shine, R., Phillips, B., Waye, H. & Mason, R. T. 2003: Small-scale geographic variation in antipredator tactics of garter snakes. Herpetologica **59,** 333—339.

Siegel, S. 1956: Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Sillén-Tullberg, B. 1990: Do predators avoid groups of aposomatic prey? An experimental test. Anim. Behav. **40,** 856—860.

Smith, S. M. 1975: Innate recognition of coral snake pattern by a possible avian predator. Science **187,** 759—760.

Sood, B., Delaney-Black, V., Covington, C., Nordstrom-Klee, B., Ager, J., Templin, T., Janisse, J., Martier, S. & Sokol, R. J. 2001: Prenatal alcohol exposure and childhood behavior at age 6 to 7 years: I. Dose-response effect. Pediatrics **108,** 1—9.

Sorci, G. & Clobert, J. 1997: Environmental maternal effects on sprint speed in the common lizard *Lacerta vivipara*. Evol. Ecol. **11,** 531—542.

Stamps, J. A. & Buechner, M. 1985: The territorial defense hypothesis and the ecology of insular vertebrates. Q. Rev. Biol. **60,** 155—181.

Sutherland, S. K. 1992: Deaths from snake bite in Australia, 1981–1991. Med. J. Aust. **157,** 740—746.

Webb, J. K., Brown, G. P. & Shine, R. 2001: Body size, locomotor speed and antipredator behaviour in a tropical snake (*Tropidonophis mairii*, Colubridae): the influence of incubation environments and genetic factors. Funct. Ecol. **15,** 561—568.

Whitaker, P. B. 1999: Behavioural ecology of the eastern brownsnake (*Pseudonaja textilis*, Elapidae) and implications for human envenomation. PhD Dissertation, Univ. of Sydney, Sydney.

Whitaker, P. B. & Shine, R. 1999a: Responses of free-ranging brownsnake (*Pseudonaja textilis*: Elapidae) to encounters with humans. Wildl. Res. **26,** 689—704.

Whitaker, P. B., Ellis, K. & Shine, R. 2000: The defensive strike of the eastern brownsnake, *Pseudonaja textilis* (Elapidae). Funct. Ecol. **14,** 25—31.