Diet divergence, jaw size and scale counts in two neighbouring populations of tiger snakes (*Notechis scutatus*)

Aubret Fabien[1,2], Xavier Bonnet[1,2], Stéphanie Maumelat[2], Don Bradshaw[2],
Terry Schwaner[4]

[1] Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France
e-mail: bonnet@cebc.cnrs.fr
[2] School of Animal Biology and Centre for Native Animal Research, University of Western Australia, Perth,
Western Australia 6009
[3] Université de Poitiers, Poitiers, France
[4] North Georgia College & State University, Dahlonega, GA 30597, USA

Abstract. Large snakes usually possess a higher number of scales to cover their larger bodies and their larger heads. It has been suggested that a diet based on large prey items also favours the development of scale number because the skin would be more extensible and would enable easier swallowing of voluminous prey. A recent study, however, suggested that although body size positively influences scale count in snakes, diet is probably unimportant (Shine, 2002). We took advantage of a natural experiment that separated two neighbouring and genetically indistinguishable populations of tiger snakes in the vicinity of Perth, Western Australia. In one population, situated on a small coastal Island (Carnac Island), snakes feed primarily on seagull chicks (large prey). In the second population, located on the mainland (Herdsman Lake), snakes feed mostly on frogs (small prey). Carnac Island snakes possess more scales (labial and mid-body rows) and larger relative jaw lengths compared with Herdsman Lake snakes. Although preliminary, these data suggest that tiger snakes, whose many populations show contrasted feeding habits, are suitable models to test the "dietary habits / scale count" hypothesis.

Introduction

Snake species eating larger prey (e.g. mammals rather than reptiles) have more supralabials and more mid-body scale rows, perhaps because an increased number of scale rows enables the skin between the scales to stretch more over large prey items (Mell, 1929a, b; Gans, 1974; Zhao and Adler, 1993; Jayne, 1988). A relatively large number of supralabial and mid-body scales could be an adaptation that enables snakes to swallow large prey. However, a comparative study based on 108 snake species challenged this simple adaptationist hypothesis (Shine, 2002). This synthesis reported the indeed interesting result that species

that eat mammals have significantly more midbody scales rows than those that feed on smaller prey such as reptiles, frogs, or invertebrates. Furthermore, the number of midbody scale rows is positively correlated with the number of supralabial scales among species. A closer analysis showed, however, that both these statistically significant effects were due to the indirect influence of body size: larger snake species possess more scales independently of their diet. Overall, the possible link between diet and number of labial and mid-body scales is questionable. At least, three processes might generate a correlation between dietary composition and scales counts in snakes (Shine, 2002).

1. Indirect effects of body size: larger snake species have more scales than smaller species (Klauber, 1956; Fitch, 1960; Arnold, 1993; Lindell, 1994; Shine, 1994) because more scales are necessary to envelop a larger body; and larger snakes can also eat larger prey (Shine, 1991).

2. Morphological adaptation to interspecific divergences in dietary habits such as relative prey size.

3. Phylogenetic inertia. Some lineages of snakes may have inherited low (or high) values for several traits simultaneously; for instance labial, dorsal scale rows and proportion of the diet composed of endotherms (large prey). For instance, most viperids exhibit high scale counts and feed on mammals whilst many natricine snakes have a low scale number and feed on amphibians. In such a null hypothesis, there is no causal relationship between scale counts and diet; numbers of scales, if adaptive, being due to some other factor (e.g., functional abilities to climb, swim, mate and/or thermoregulate).

Being not mutually exclusive, these hypotheses are difficult to tease apart (i.e. adaptation versus exaptation). The co-evolution of large size and scalation in response to diet may be so tight, or so noisy, that analysis of covariance may not allow disentangling the causality among the different elements of the system. Experimental data would be very useful to clarify the situation; but may well prove to be extremely difficult to obtain due the expected very long time scale to modify artificially scale count via selection based solely on diet. Comparisons, at the species level to limit phylogenetic inertia, among populations that feed on different prey items offer an alternative natural experiment and provide an opportunity to explore the "dietary habits / scale count" hypothesis. In this paper we report data gathered on two populations of western tiger snakes that exhibit extremely divergent diets. We also report results on relative jaw length, another trait supposedly important for swallowing capacities in gape-limited predators (Shine, 1991).

Materials and methods

Study areas

We studied two neighbouring populations (separated by roughly 25 km in a straight line) of tiger Snakes (Cogger, 1992) in Western Australia situated respectively on Carnac Island (hereafter CI) and Herdsman Lake (hereafter HL). Individuals from the two populations have been recently sampled for DNA analyses (1999, 2000). The

results failed to detect any divergence between them (less than 0.3% in a matrix of genetic [5 mitochondrial genes, 4825 base pairs] distances between CI and other Western Australia mainland tiger snakes; Scott et al., 2001; Keogh et al., unpublished). Importantly, these results do not show that both populations have not diverged in un-sampled alleles, for example those that are involved in the control of scalation and/or differential growth rates of the different parts of the head. This brings caution in the interpretation of our results, notably to tease apart the effect of plasticity versus adaptation; the main conclusions (differential diets may influence morphology) will not be altered however. Despite their strong genetic similarities, the populations live in very different environments and exhibit marked phenotypic divergences (Bonnet et al., 2002) suggesting a strong effect of phenotypic plasticity. A previous study showed that, although body sizes largely overlap between the two populations, adult Carnac Island snakes are larger on average than Herdsman Lake snakes (Bonnet et al., 2002). In this independent data set, excluding juveniles from analyses, we found similar results (see Results).

Carnac Island (CI) is approximately 12 km off the coast of Perth ($32°07'$S; $115°39'$E). The island was formed approximately 6,000 years ago by rising sea levels (Seddon, 1972). No frogs occur on Carnac Island. Skinks and mice constitute the major diet components of neonate and juvenile snakes, whereas the adults feed mostly on silver gull chicks (Bonnet et al., 1999; this study). Herdsman Lake (HL; $31°55'44''$S; $115°48'19''$E) is a natural reserve in Perth. A lake constitutes a favourable habitat for several frog species (i.e. *Litoria moorei*, *Litoria adelaidensis, Crinia insignifera*). HL tiger snakes do not feed on sea-gull chicks, as this bird does not nest in this area. Although the largest snakes in HL may potentially eat the chicks of ducks and grebes (no records however), frogs and mice are by far the more accessible prey and constitute their main diet (see Results). Based on more than 290 prey items in CI snakes, sea gull chicks represent 83% of the prey; mice 15% and lizards 2% respectively (Bonnet et al., 1999). Overall, CI snakes feed mostly on seagull chicks, especially during adulthood.

Snake morphology

Between September 2001 and April 2002, 238 tiger snakes were captured, 142 in Herdsman Lake (21 juveniles and 121 adults), and 96 on Carnac Island (5 juveniles and 91 adults). Each snake was sexed by eversion of the hemipenes, and individually marked by scale-clipping. Snout vent length (SVL) and total body length were recorded to the nearest 0.5 cm, body mass was recorded to the nearest 1 g with a portable electronic scale.

Between November 2001 and February 2002, we captured 13 pregnant females (5 from CI and 8 from HL), and kept them in individual cages in the laboratory until parturition in a controlled temperature room ($27°$C by day and $20°$C by night). Water was provided *ad libitum* and food (dead mice) approximately every 3 weeks. Parturition occurred between the 17 March 2002 and 18 May 2002. Data were collected for 135 neonates, 57 from CI (35 alive and 22 stillborn) and 78 from HL (54 alive and 24 stillborn).

For each snake, we scored the number of labial and mid-body scales. We counted both the number of supra and infra labial scales. The number of mid-body scale rows was counted on two different sections of the body to limit errors due to scale abnormalities. We also measured the size of the mouth (from the tip of the nose to the rear edge of the last supralabial scale), and jaw length (from the tip of the nose to the articulation of upper jaw; using a digital calliper, precision 0.01 mm).

Diet

Prey items were identified either by palpation of the snake's abdomen (mice, lizards and chicks are easily differentiated by their shape) or from remains in faecal samples. Some snakes regurgitated their prey during handling, and in all cases, palpations had correctly identified both the prey species and number. One snake on CI was captured when feeding on a wedge-tailed shearwaters chick (*Puffinus pacificus*). A total of 13 prey items were identified in HL snakes, with frogs composing 62.5% (5 in adults versus 3 in juveniles) and mice 37.5% (5 in adults versus none in juveniles) of prey items.

The average body size of the several prey types consumed by the snakes was obtained from preserved specimens under the care of the WA Museum (*Egernia kingii*; *Ctenotus fallens*; *Litoria moorei* and *Crinia insignifera*). Another frog (*Litoria adelaidensis*) was measured directly in the field in Ti Tree Lake (15 km south of Perth). We measured snout-vent length, body mass and maximal circumference (either around the head or around the body, depending upon the species' body shape) of all potential prey (Greene, 1983, 1997; Shine, 2002). For our purpose, prey circumference is likely to be the most appropriate measure linked to snake's body distension (hence skin stretching) during prey ingestion.

Results

Snake morphology

Average snout vent length of CI snakes was 90.16 ± 10.14 cm versus 79.32 ± 7.53 cm for HL snakes (one factor Anova with population as the factor and SVL as the dependent variable; $F_{1,210} = 79.65$; $P < 0.0001$). CI island snakes were heavier (same design Anova, excluding snakes with a prey in the stomach or gravid females; 431.96 ± 130.56 g versus 250.29 ± 71.35 g; $F_{1,206} = 163.80$; $P < 0.0001$). They also exhibited higher body condition values relative to HL snakes (residuals values from the Ln-Body Mass / Ln-Snout Vent Length regression: respectively 0.038 ± 0.076 versus -0.029 ± 0.079; Ancova with body mass as the dependent variable and SVL as a covariate; $F_{1,205} = 66.2$; $P < 0.0001$). These trends remained unchanged when the effect of sex was incorporated into the analyses to take into account the different sex ratio (although not significant in our sample with 32% of females on CI and 36% on HL: $\chi^2 = 0.46$, df $= 1$, $P = 0.50$) between the two populations, as in subsequent results.

CI snakes have significantly more supralabials than HL snakes (respectively 6.12 ± 0.32 versus 5.68 ± 0.67, $F_{1,168} = 28.28$, $P < 0.0001$). The number of infralabial scales was however not significantly higher in CI snakes (respectively 7.11 ± 0.35 versus 7.03 ± 0.36; $F_{1,168} = 1.78$, $P < 0.18$) compared with HL snakes. The number of midbody scales rows is also higher in CI snakes compared with HL snakes (respectively 18.94 ± 0.28 versus 17.45 ± 0.77, $F_{1,211} = 291.97$, $P < 0.0001$). The number of scales is fixed at birth and we compared only two populations in this study (a positive correlation is inevitable but not informative), hence we did not use Ancova to control for a potential effect of body size on scalation for these analyses.

Head size (jaw and mouth size) was positively correlated with body size (multiple regression; $R = 0.94$, $n = 169$, $P < 0.0001$). As a consequence of their larger body size, CI snakes exhibited longer absolute jaw (32.83 ± 4.22 mm versus 28.19 ± 3.03 mm; same design Anova $F_{1,229} = 94.58$, $P < 0.0001$) and mouth length (29.74 ± 3.70 mm versus 26.07 ± 2.86 mm; same design Anova $F_{1,168} = 52.01$, $P < 0.0001$) when compared to HL snakes. Interestingly, CI also possessed larger relative jaw length when the difference in body size was taken into account (size corrected jaw length were 31.28 ± 4.21 mm versus 29.741 ± 3.04 mm respectively for CI and HL snakes; Ancova with SVL as the covariate, Slopes, $F_{1,227} = 0.54$, $P = 0.46$; Intercepts, $F_{1,228} = 52.80$, $P < 0.0001$). A similar result was found for relative mouth length (size corrected mouth length was 28.25 ± 3.71 mm in CI snakes and 27.55 ± 2.86 mm in HL snakes; Slopes, $F_{1,222} = 0.98$, $P = 0.32$; Intercepts, $F_{1,121} = 10.38$, $P < 0.0015$).

Feeding habits

The respective diet of the two populations differed significantly ($\chi^2 = 39.76$, df $= 3$ $P < 0.0001$).

Table 1. Morphological characteristics of the preys consumed by CI and HL snakes.

Species	BM (g)	SVL (cm)	Circumference (mm)	n
Puffinus pacificus (CI)	133.1	17	155	1
Larus novaehollandiae (CI)	39.70 ± 4.97	13.64 ± 1.48	121.80 ± 13.12	10
Egernia kingii (CI)	26.43 ± 16.10	10.63 ± 3.58	58.42 ± 14.56	21
Mus musculus (CI and HL)	19.28 ± 4.21	10.00 ± 2.36	55.82 ± 8.83	28
Litoria insignifera (HL)	18.64 ± 12.23	6.38 ± 1.02	58.85 ± 9.47	21
Ctenotus fallens (HL)	9.85 ± 6.03	7.38 ± 1.69	33.45 ± 9.33	40
Crinia moorei (HL)	1.00 ± 0.25	1.94 ± 0.23	21.55 ± 4.33	20
Litoria adelaidensis (HL)	0.88 ± 0.59	6.97 ± 9.99	21.76 ± 4.24	33

Note: Analysis showed that maximum circumference was reached at midbody rather than head in both skink species (*Ctenotus fallens* midbody: 33.45 ± 9.34 mm versus head: 29.77 ± 6.46 mm; ANOVA; $F_{1,78} = 4.20$; $P < 0.044$; *Egernia kingii* midbody: 57.36 ± 15.47 mm versus head: 49.00 ± 11.06 mm; ANOVA; $F_{1,42} = 4.25$; $P < 0.045$).

Prey size

Morphometric data collected on the potential preys eaten by the snakes are presented in table 1. The three larger prey items (disregarding the house mice which occurs both in HL and CI) occurs on CI: *Puffinus pacificus*, *Larus novaehollandiæ*, and *Egernia kingii* are significantly larger in BM (respectively 29.92 ± 15.26 g versus 7.32 ± 9.18 g; ANOVA, $F_{1,140} = 185.75$; $P < 0.0001$), SVL (respectively 11.61 ± 3.36 versus 6.12 ± 5.77; ANOVA, $F_{1,139} = 34.72$; $P < 0.0001$); and in circumference (respectively 77.34 ± 33.75 mm versus 32.66 ± 15.44 mm; ANOVA, $F_{1,140} = 741.42$; $P < 0.0001$).

Discussion

Contrasted life history traits (i.e. body size, sexual size dimorphism, adult sex-ratio) have been documented among distinct populations of tiger snakes; mostly between mainland and islands (Shine, 1977, 1978, 1987; Schwaner, 1985, 1990, 1991; Schwaner and Sarre, 1988, 1990). These variations have been interpreted as consequences of differences in prey abundance and relative prey size availability (Schwaner, 1985; Shine, 1987). In all mainland populations sampled amphibians were the main prey consumed (50-81% of the records) whereas the proportion of endothermic prey was much lower (14-41%). By contrast, island tiger snakes feed mostly on relatively large endotherms (66% of the preys were bird chicks and mice), frogs being less represented (about 23%). The dietary divergence was particularly marked, however, with almost no overlap in the species and relative prey size consumed at both sites. Silver gull chicks are the main prey item on Carnac Island but are not eaten by HL snakes; frogs are the main prey items in Herdsman Lake, but CI snakes never consume them.

Our results are consistent with the notion that snakes that feed on larger prey items tend to exhibit higher values for the number of midbody scales rows and supralabial

scales and a greater relative jaw length relative to SVL; these traits supposedly help to swallow large prey item such as those consumed by CI snakes. However, rather than being adaptive (i.e. genetically determined), some of the patterns we observed may reflect instead a direct effect of food availability on relatively plastic feeding structures. When imposed over a prolonged time period, contrasting experimental diets may lead to divergent relative jaw length (Forsman and Lindell, 1993; Forsman, 1996; Forsman and Shine, 1997 versus Queral-Regil and King, 1998; Bonnet et al., 2001 for a discussion). Although phenotypic plasticity may explain why CI snakes attain larger body size and develop a larger relative jaw length when compared with HL snakes; the difference in scalation between the two populations is less likely to respond directly to diet but rather to selection. Indeed, scalation is fixed at birth (Pasteur, 1977).

Several limits impose important cautions to our study however. Firstly, although probably not confounded by strong phylogenetic distances, our analyses are based on the comparison between two populations only. In the future, it would be informative to extend the investigations to other sites; for example to incorporate other populations that exhibit marked diet divergences, either in tiger snakes (Shine, 1987; Schwaner and Sarre, 1988, 1990) or other species (e.g. Carpet pythons contain distinct populations that feed on small versus large preys; Pearson et al., 2002). Indeed, such studies should be analysed using the same comparative methods that take phylogenetic relationships into account: within and between species, with data being incorporated into the same statistical account. Secondly, some of the many uncontrolled environmental factors affecting the two populations may have caused the differences in scale count and relative jaw size independently of the diet. For example, in snakes, scalation is sensitive to the temperatures experienced by the embryos during their development (Fox, 1948; Osgood, 1978; note that the differences found by these authors were very small and almost systematically related to the occurrence of anomalies). Hence, we cannot exclude a possible effect of climatic divergences between our two study sites (island versus "city" climate), but the difference cannot be great in our case due to the proximity of the two sites. However, we obtained the same count differences between neonates from litters of CI and HL females kept in similar conditions in the laboratory during pregnancy (table 2) discarding a temperature effect on scalation as a major factor on our results. Thirdly, Cann's (1986) reported that 80 snakes were released on CI in 1929, but did not mention that at least some of those snakes came from eastern Australia (pers. com., Glen Storr (dec.) to Terry Schwaner, December, 1986), and we have no information about the possible genetic contribution of these introduced snakes to the current CI population. Tiger snakes from eastern Australia (east of the Great Divide) have a similar number of scale rows at midbody compared with CI snakes (table 3), but they are nonetheless genetically distinct from WA snakes (comparing populations across Australia, a maximum overall genetic distance of 1.4% was found between WA tiger snakes and other eastern populations of tiger snakes; Keogh et al., unpublished). Consequently, the differences in scale rows at midbody detected between CI and western Australian mainland tiger snakes cannot be attributed to a causal mechanisms with certainty as the respective

Table 2. Neonate's scalation and size-adjusted-jaw-length (dependent variables) were compared using mixed model Ancovas with snake's origin as the main factor and maternal identity as a random factor. Means are given with S.E. and sample size in brackets. Values observed in the adults are indicated in square brackets.

Origin	Supra Labials	Infra Labials	Mid Body scales	Adjusted Jaw Length
Carnac Island	6.20 ± 0.41 (35)	7.14 ± 0.36 (35)	18.36 ± 0.90 (33)	13.85 ± 0.11 (35)
	[6.12 ± 0.32]	[7.11 ± 0.35]	[18.94 ± 0.28]	
Herdsman Lake	5.76 ± 0.64 (54)	6.65 ± 0.65 (54)	17.06 ± 0.52 (49)	13.25 ± 0.09 (54)
	[5.68 ± 0.67]	[7.03 ± 0.36]	[17.45 ± 0.77]	
F	6.21	6.31	94.96	2.77
df	1, 11	1, 11	1, 12	1, 11
P	0.0496	0.0425	0.0060	0.1238

Table 3. Midbody scale counts (mean ± s, sample size in brackets) on tiger snakes were performed by one of us (T. Schwaner) twenty years before the current survey. WA (CI and Perth area) counts are based on specimens kept in the Western Australian Museum and taken from the Perth area prior to 1986, but after 1929.

Origin	Mid Body scales
Carnac Island	18.75 ± 0.59 (28)
Perth Area	17.66 ± 0.90 (73)
New South Wales	18.62 ± 0.86 (76)

influence of introduced snakes from eastern Australia versus adaptation to prey size (that may have occurred either before or after the introduction) remain unclear.

Despite such uncertainty, these results provide a clear support to the notion that scale count can be modified relatively independently from broad inter-population divergences (WA versus others) in tiger snakes. Overall, although preliminary, our data suggest that further investigations should be conducted within species, in addition to among species comparisons, to better appreciate the diet/scale count hypothesis, especially because scalation is a potential target of natural selection in snakes (Pasteur, 1977; Arnold and Bennett, 1988; Dohm and Garland, 1993; Shine, 2000).

References

Arnold, S.J. (1993): Foraging theory and prey-size-predator-size relations in snakes. In: Snakes. Ecology and Behavior, p. 87-116. Seigel, R.A., Collins, J.T., Eds, New York, McGraw-Hill.

Arnold, S.J., Bennett, A.F. (1988): Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake *Thamnophis radix*. Biological Journal of the Linnean Society **34**: 175-190.

Bonnet, X., Bradshaw, S.D., Shine, R., Pearson, D. (1999): Why do snakes have eyes? The (non-)effect of blindness in island tiger snakes. Behavioural Ecology and Sociobiology **46**: 267-272.

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

Bonnet, X., Shine, R., Naulleau, G., Thiburce, C. (2001): Plastic vipers: influence of food intake on the size and shape of Gaboon vipers, *Bitis gabonica*. Journal of Zoology, London **255**: 341-351.

Cann, J. (1986). Snakes Alive. Sydney, Kangaroo Press.

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

Dohm, M.R., Garland, T. Jr (1993): Quantitative genetics of scale counts in the garter snake *Thamnophis radix*. Copeia **1993**: 987-1002.

Fitch, H.S. (1960): Autecology of the copperhead. University of Kansas Publications of the Museum of Natural History **13**: 85-288.

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

Forsman, A., Lindell, L.E. (1993): The advantage of a big head: swallowing performance in adders, *Vipera berus* (L.). Functional Ecology **7**: 183-189.

Forsman, A., Shine, R. (1997): Rejection of non-adpatative hypotheses for intraspecific variation in trophic morphology in gape-limited predators. Biological Journal of the Linnean Society **62**: 209-223.

Fox, W. (1948): Effect of temperature on development of scutellation in the gerter snake, Thamnophis elegans atratus. Copeia **1948**: 252-262.

Gans, C. (1974): Biomechanics: An Approach to Vertebrate Biology. Philadelphia, J.P. Lippincott.

Greene, H.W. (1983): Dietary correlates of the origin and radiation of snakes. American Zoologist **23**: 431-441.

Greene, H.W. (1997): Snakes. The evolution of mystery in nature. Berkeley, CA, University of California Press.

Jayne, B.C. (1988): Mechanical behaviour of snake skin. Journal of Zoology, London **214**: 125-140.

Klauber, L.M. (1956): Rattlesnakes. Their Habits, Life Histories and Influence on Mankind. Berkeley, University of California Press.

Lindell, L.E. (1994): The evolution of vertebral number and body size in snakes. Functional Ecology **8**: 708-719.

Mell, R. (1929a): Beiträge zur Fauna Sinica. IV. Grundzüge einer Ökologie der Chinesischen Reptilien und einer Herpetologischen Tiergeographie Chinas. Berlin, Walter de Gruyter.

Mell, R. (1929b): Preliminary contributions to an ecology of East Asiatic reptiles, especially snakes. Lingnan Science Journal **8**: 187-197.

Osgood, D.W. (1978): Effects of temperature on hte development of meristic characters in *Natrix fasciata*. Copeia **1978**: 33-47.

Pasteur, G. (1977): Endocyclic selection in reptiles. American Naturalist **111**: 1027-1030.

Pearson, D., Shine, R., How, R. (2002): Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). Biological Journal of the Linnean Society **77**: 113-125.

Queral-Regil, A., King, R.B. (1998): Evidence for phenotypic plasticity in snake body size and relative head dimensions in response to amount and size of prey. Copeia **1998**: 423-429.

Seddon, G. (1972): Sense of Place. Nedlands, WA, University of Western Australia Press.

Schwaner, T.D. (1985): Population structure of black Tiger snakes, *Notechis ater niger*, on offshore islands of South Australia. In: Biology of Australian Frogs and Reptiles, p. 35-46. Grigg, G.C., Shine, R., Ehmann, Eds, Sydney, Royal Zoological Society of New South Wales.

Schwaner, T.D. (1990): Geographic variation in scale and skeletal anomalies of tiger snakes (Elapidae: *Notechis scutatus-ater* complex) in southern Australia. Copeia **1990**: 1168-1173.

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

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

Schwaner, T.D., Sarre, S.D. (1990): Body size and sexual dimorphism in mainland and island Tiger Snakes. Journal of Herpetology **24**: 320-322.

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*. Molecular Ecology Notes **1**: 117-119.

Shine, R. (1977): Habitats, diets and sympatry in snakes: A study from Australia. Canadian Journal of Zoology **55**: 1118-1128.

Shine, R. (1978): Growth rates and sexual maturation in six species of Australian Elapid snakes. Herpetologica **34**: 73-79.

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

Shine, R. (1991): Why do larger snakes eat larger prey items? Functional Ecology **5**: 493-502.

Shine, R. (1994): Allometric patterns in the ecology of Australian snakes. Copeia **1994**: 851-867.

Shine, R. (2000): Vertebral numbers in male and female snakes: the roles of natural, sexual and fecundity selection. Journal of Evolutionary Biology **13**: 455-465.

Shine, R. (2002): Do dietary habits predict scale counts in snakes? Journal of Herpetology **36**: 268-272.

Zhao, E., Adler, K. (1993): Herpetology of China. Oxford, Ohio, Society for the Study of Amphibians and Reptiles.