Feeding preferences in 2 disjunct populations of tiger snakes, *Notechis scutatus* (Elapidae)

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Variations at both the genetic and phenotypic levels play an important role in responses to food and food-related stimuli. Knowledge of such variations is crucial to understanding how populations adapt to changing environments. We investigated the dietary preferences of 2 tiger snake populations and compared the responses of diet-naive animals (laboratory-born neonates), diet-controlled animals (laboratory-reared juveniles), and natural diet–experienced animals (wild-caught adults) to visual and chemical cues from 6 prey types (mouse, skink, silver gull, chicken, shearwater, and frog). The mainland population inhabits a swamp, feeds mostly on frogs, and suffers heavy predation. The second population inhabits a small nearby offshore island with no standing water (no frogs); feeds mostly on skinks, mice, and, as adults, silver gull chicks; and suffers no known predation. Although different prey are eaten in the 2 populations, adult wild-caught snakes from both populations showed a significant preference for 3 types of prey (frog, mouse, and chick), irrespective of their natural diet. Neonates responded to all prey cues more than they did to control stimuli in both populations. However, the island neonates showed significantly higher interest in silver gull chick stimuli (the main prey of the island adult snakes) than did their mainland conspecifics. Laboratory-bred juveniles displayed behavioral plasticity by significantly increasing their response to mice after being fed baby mice for 7 months. We conclude that genetic-based differences in food-related cues are important in tiger snakes but that they are also capable of behavioral plasticity. Island adult and neonate snakes exhibited responses to prey types no longer consumed naturally (frog), suggesting that behavioral characters may have been retained for long periods under relaxed selection. Island neonates showed a strong interest in a novel prey item (silver gull). This result complements previous work describing how island snakes have developed the ability to swallow larger prey than usual, as well as seemingly developing a taste for them. *Key words:* island, *Notechis*, plasticity, preferences, prey, snake. *[Behav Ecol 17:716–725 (2006)]*

Comparisons of conspecific populations can be effective in elucidating selective pressures and adaptive causes of differentiation in animal behavior because confounding variables are not as prevalent and small evolutionary steps can be revealed (Foster and Endler 1999). Comparisons between conspecific populations are also useful in understanding the evolutionary significance of phenotypic plasticity (e.g., Schlichting and Pigliucci 1995; Via et al. 1995; Wagner and Altenberg 1996; Aubret, Shine, and Bonnet 2004). Knowledge of genetic–environment interactions in behavior within natural populations is crucial to our understanding of how populations adapt to changing circumstances. However, measuring such interactions within natural populations has proved difficult (Plomin and Hershberger 1991).

Dietary selection is a major arena for the operation of behavioral plasticity, and it is known that both genetic and phenotypic variations play important roles in molding responses to food and food-related cues (Falciglia and Norton 1994; Segal and Topolski 1995). The role of early experiences can be particularly profound and influence chemoreceptive and feeding responses in birds (Marchetti and Price 1989), fishes (Croy and Hughes 1991), insects (Kral 1998), as well as reptiles (Burghardt 1993; Mori 1996; Burghardt and Krause 1999; Krause and Burghardt 2001). Intraspecific variation, on the other hand, may reflect microevolutionary processes related to geographical differences in available prey, predators, or interspecific competition for resources (Burghardt 1970; Arnold 1981a, 1981b; Burghardt and Schwartz 1999; Cooper et al. 2000). The quantitative genetics of the initial responses of diet-naive or prey-naive snakes is well established (Brodie and Garland 1993), but given the demonstration of experience and prey-type interactions (e.g., Burghardt et al. 2000), the microevolutionary consequences of selection on older animals may underestimate both the rate of microevolution (Resnick et al. 1997) and the role of experience and ontogenetic processes in evolutionary events (Burghardt et al. 2000).

Geographical separation of conspecific populations of predatory snakes offers opportunities to investigate evolutionary mechanisms of dietary preferences. Notably, interspecific differences in chemosensory preferences in neonatal snakes may reflect species-typical diets (Burghardt 1969, 1993) or the retention of ancestral diet-specific preferences (Burghardt 1967; Coss 1999). Responses to prey chemical cues at birth are heritable in several species of snakes (reviews in Arnold 1981c; Brodie and Garland 1993), are often modifiable with feeding experience (Burghardt 1993), and show significant interactions with experience (Burghardt et al. 2000).

In order to better understand the relative importance of genes, experience, and ontogenetic processes on feeding preferences, we studied 2 nearby, but disjunct, populations of tiger snakes, *Notechis scutatus*, from Western Australia. As described below, the 2 populations appear genetically very similar but live in differing environments with different available prey and different diets as confirmed by field studies (Aubret, Bonnet, et al. 2004). The potential for plasticity in these 2 populations

has been revealed, notably behaviorally (Aubret 2004; Aubret, Shine, and Bonnet 2004; Bonnet et al. 2004).

Snakes have a well-developed chemoreceptive organ, the vomeronasal organ, situated in the roof of the oral cavity (Halpern 1992). Snakes transport chemicals (vomodors) from the environment to this organ via the tongue as it flicks (Halpern 1992). Snakes will often emit more tongue flicks and even attack items such as cotton swabs containing aqueous chemicals from species-typical prey. The term "preference" has been applied to situations in which chemical or other cues from one prey are responded to relatively more than another (Burghardt 1967).

We investigated the prey preferences of both populations using prey-naive neonates, juveniles reared on a controlled diet, and wild-caught adults. We attempted to answer the following questions. Are feeding preferences similar at birth between the 2 populations, or can effects of selection be detected over time? Are ancestral preferences still present in the isolated population? What is the role of experience in the expression of feeding preferences, especially toward novel types of prey?

METHODS

Species

Highly venomous Australian tiger snakes, *N. scutatus* (Elapidae), are found in all southerly parts of Australia, including Tasmania. Mainland tiger snakes feed principally on frogs, which constitute 50–81% of all prey items recorded, whereas the proportion of endotherms (small mammals) is much lower (14–47%; Shine 1977, 1987; Aubret, Bonnet, et al. 2004). By contrast, tiger snakes on islands typically eat far fewer frogs (23%) and more endotherms (66%).

Study sites

We studied 2 populations separated by 25 km in Western Australia: Carnac Island and Herdsman Lake.

Carnac Island is a small limestone plateau surrounded by sand beaches (total area of 16 ha), located approximately 12 km off the coast of Fremantle (32°07′S, 115°39′E). The island was formed some 6000 years ago by rising sea levels (Seddon 1972). The vegetation of the island was described by Abbott (1978, 1980). There are no freshwater sources available except rainfall or dew, and no frogs occur on Carnac Island. Although several bird species, including pied cormorants (*Phalacrocorax varius*), little penguins (*Eudyptula minor*), and wedge-tailed shearwaters (*Puffinus pacificus*), nest on Carnac, the silver gull (*Larus novaehollandiae*) is by far the most abundant bird species (Lane 1979). Large skinks (*Egernia kingii*) are common, and smaller skinks (*Morethia obscura*) also occur on Carnac Island (Bush et al. 1995). The only mammals are house mice (*Mus musculus*) and sea lions (*Neophoca cinerea*) (Abbott 1978; Young 1981). Skinks and mice constitute the major diet components of neonate and juvenile snakes, whereas the adults feed mostly on silver gull chicks (83% of the prey; Bonnet et al. 2002; Aubret, Bonnet, et al. 2004), with mice (15%) and lizards (2%) constituting the remainder. There is one record of a wedge-tailed shearwater chick being eaten. However, field observations suggest that the proportion of shearwater chicks in the diet of adults may be underestimated because few research trips to the island coincided with the nesting period of this bird.

Herdsman Lake (31°55′44″S, 115°48′19″E) is a natural reserve in Perth. A dredged moat encircling the 300-ha lake ensures permanent open water. It is composed of artificial banks and paths sometimes bordered by trees that create a mosaic of vegetation patches (mostly reeds) and a net of interconnected shallow freshwaters. The lake constitutes a favorable habitat for several frog species (*Litoria moorei*, *Litoria adelaidensis*, and *Crinia insignifera*). Long-neck turtles (*Chelodina longicollis*), domestic and feral cats, and house mice (*M. musculus*) also occur in Herdsman Lake. Herdsman Lake tiger snakes do not feed on seagull chicks as this bird does not nest in the area. Although the largest snakes in Herdsman Lake could potentially eat the chicks of ground-nesting ducks and grebes, there are no records of this occurring. Frogs and mice are far more accessible prey and constitute 53% and 47%, respectively, of all prey items (Aubret, Bonnet, et al. 2004).

Recent mitochondrial DNA (mtDNA) genetic studies on snakes from these 2 populations and others (years 1999 and 2000) found little divergence (less than 0.3%) in a matrix of genetic distances (5 mitochondrial genes, 4825 base pairs) between Carnac Island and other Western Australian mainland tiger snakes, including the Herdsman Lake population (Scott et al. 2001; Keogh et al. 2005). Carnac Island and Herdsman Lake tiger snake populations are nevertheless morphologically distinguishable (Bonnet et al. 2002; Aubret, Bonnet, et al. 2004), suggesting that tiger snakes exhibit phenotypic plasticity or, alternatively, that the portion of mtDNA sampled does not detect subtle differences between populations. For instance, Carnac Island adults average 11% longer in snout–vent length and 100% heavier in mass compared with Herdsman Lake individuals. Carnac Island snakes also have more midbody scale rows, have more infra- and supralabials, and possess larger jaws relative to body size. These characters are possibly related to the fact that Carnac Island individuals feed on larger prey than Herdsman Lake individuals (see Aubret, Bonnet, et al. 2004; Aubret, Shine, and Bonnet 2004). The origin of tiger snakes on Carnac Island remains unclear. It is possible that the population may be derived, at least in part, from individuals marooned by the rising sea level 5000–7000 years ago when Carnac was separated from the mainland. However, Cann (1986) stated that a founder population of some 80 mainland individuals was released on the island around 70 years ago. Department of Conservation and Land Management records indicate that this introduction occurred around 1929. In either case, Carnac Island and Herdsman Lake snakes are undoubtedly closely related to each other.

Experimental methods

Several experiments were conducted on different groups of snakes. The following general details apply to these experiments.

Testing order

Test order and prior experience may determine subsequent behavior (Burghardt 1969; Arnold 1992; Burghardt and Schwartz 1999). The order of presentation of food items was thus systematically balanced among individuals within both populations: on testing day 1, snake 1 was presented stimulus 1, snake 2 stimulus 2, snake 3 stimulus 3, and so on. On testing day 2, snake 1 was presented stimulus 2, snake 2 stimulus 3, snake 3 stimulus 4, and so on for N different stimuli and N snakes, depending on the experiment.

Data analyses

A value of +1 was added to all tongue flick scores and time scores, and both were LN transformed prior to analysis. With multiple measures (different prey items and control) on same individuals within each population, we used Friedman analyses of variance (ANOVAs) (experiment 1). Wilcoxon matched signed-rank tests were used in the choice experiments in adults (experiment 2). In tests where bites were observed

Table 1

Morphological comparison at birth and as adults between the 2 populations

Traits	Carnac Island	Herdsman Lake	df; F	P
Adults				
Body mass (g)	376.02 ± 139.05	226.03 ± 102.38	1,53; 20.86	0.001
Snout–vent length (cm)	84.50 ± 12.27	75.89 ± 13.28	1,53; 6.22	0.016
Body condition	0.044 ± 0.061	−0.043 ± 0.061	1,53; 28.23	0.001
Neonates				
Body mass (g)	6.70 ± 0.82	4.25 ± 0.86	1,82; 168.76	0.001
Snout–vent length (cm)	20.52 ± 1.19	16.98 ± 1.34	1,82; 150.34	0.001
Body condition	0.0085 ± 0.051	0.0052 ± 0.043	1,82; 1.70	0.20

Nested ANOVA were used in neonates to account for potential maternal effect, with factor litter nested into population and the relevant trait as the dependent variable. df, degrees of freedom.

(experiments 3 and 4), we used the standard composite tongue flick attack score (hereafter TFAS) for repeated measures to account for the shortened trials when actual attack and ingestion attempts occurred (Cooper and Burghardt 1990). Detailed analysis within each population for each pair of stimuli was performed using Duncan's new multiple range tests. Several litters of neonates were tested on each prey item for each population. Replicate litter and maternal effects were controlled by using nested ANOVAs with "litter" nested into "prey items" (experiments 3 and 4) and with "litter" nested into "population" (experiment 3). TFAS at 6 weeks and 8 months for the same individuals were compared using Wilcoxon matched-pairs tests (experiment 4).

Differences in overall level of responsiveness to the control stimuli differed between the 2 populations (scores for control were typically higher in Carnac Island individuals, in adults as well as in neonates). Hence, in order to compare the scores (tongue flick scores, time scores, and TFASs) between the 2 populations, we performed for each different prey item a repeated-measures ANOVA with population as factor, "LN score of the control" as the first measure, and "LN score of prey item" as the repeated measure. For instance, to compare the tongue flick scores for "mouse" between Carnac Island and Herdsman Lake adult snakes, we used population as factor, LN (tongue flick scores) of "control" as the first measure, and LN (tongue flick scores) for "mouse" as the second measure. The level of significance of the interaction term population × scores indicated if the 2 populations differed in their response for a given prey item, independent of their level of responsiveness.

Feeding preferences in field-caught adult tiger snakes

Subjects

A total of 55 adult tiger snakes were captured in the wild, 16 males and 11 females from Carnac Island and 17 males and 11 females from Herdsman Lake. Snout–vent length was recorded to the nearest 0.5 cm. Body mass was recorded to the nearest 1 g with an electronic scale. A body condition index was calculated for each snake, using the residual values of the linear least squares regression of log (body mass) against log (snout–vent length). Such an index provides accurate estimates of body reserves (fat and muscle) in snakes (Bonnet and Naulleau 1994). These morphological data are presented in Table 1.

Maintenance

Snakes were individually housed in plastic boxes (50 × 40 × 30 cm), with shelter and paper toweling and water provided ad libitum. Because mice are the only natural prey shared by Herdsman Lake and Carnac Island snakes, all snakes were offered dead mice approximately every 3 weeks. At least 15 days lapsed between feeding and testing. Feeding tests took place between October 2001 and January 2002. The experimental room was set at 27.5 °C by day and 20 °C by night. All tests were performed at approximately 27 °C as the average body temperature chosen by both Herdsman Lake and Carnac Island snakes in captivity is 26.8 ± 0.7 °C (Ladyman and Bradshaw 2003).

Experimental design

The testing environment was a 90 × 40 × 50–cm glass terrarium (see Figure 1). A sliding door partitioned the terrarium into 2 equal compartments, and a wooden board covered the top. All sides were covered with paper to avoid disturbance to the snake, and a small window (5 × 5 cm) in the paper allowed for observations.

The snake was placed in one side of the terrarium. In the center of the other compartment, a live prey animal was placed under a steel strainer (10-cm diameter, 7 cm deep, mesh size of 1 mm) and taped to the floor. Each strainer
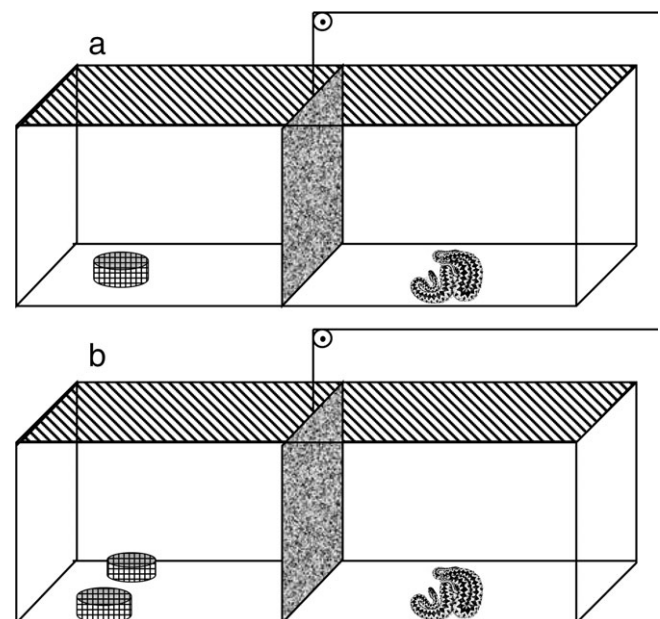
Figure 1
Diagram represents the testing terrarium used for the investigation of prey preferences in adult tiger snakes, with a single prey (a) or a choice of 2 prey (b).
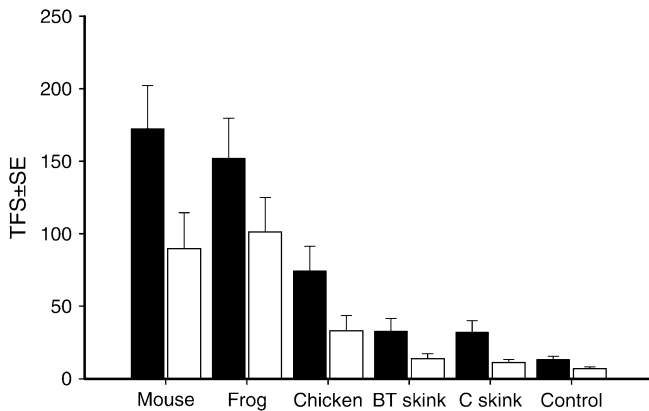
Figure 2
Graph represents the tongue flick scores (mean ± standard error) in response to prey stimuli in 27 Carnac Island (filled bars) and 28 Herdsman Lake (open bars) adult tiger snakes.
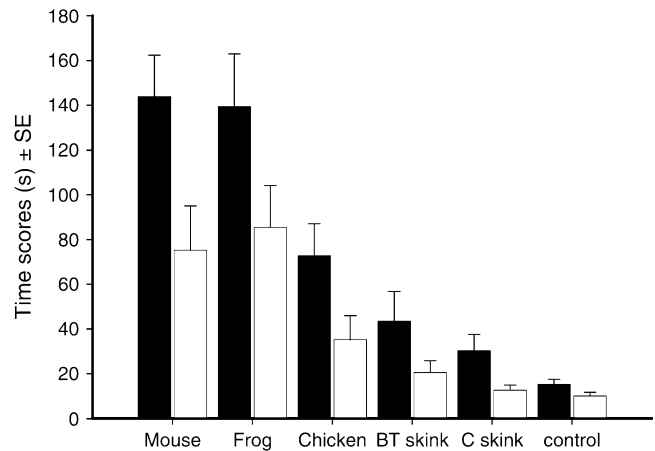
Figure 3
Graph represents the time scores (mean ± standard error) in response to prey stimuli in 27 Carnac Island (black charts) and 28 Herdsman Lake (white charts) adult tiger snakes.

was associated with one prey type, and prior to the experiment, the body of each prey was gently rubbed onto the whole surface of its strainer.

After introduction into the empty compartment, snakes were allowed to habituate for approximately 15 min. The sliding door was then lifted with a remotely operated rope and pulley system. As soon as the snake's head entered the test compartment containing the prey, data recording commenced for a 10-min period. We recorded the time spent by the snake orienting tongue flicks (hereafter time scores) toward the strainer and scored the number of tongue flicks directly contacting the strainer (hereafter tongue flick scores). After each experiment, the whole terrarium was cleaned with soap and bleach to remove all odor cues, rinsed, and then allowed to dry before the next trial. Prey species were always kept in a separate room so as not to introduce mixed odors to the experimental room or accustom the snakes to ambient odors (Burghardt and Layne 1995).

Experiment 1. Tests on adult snakes with a single prey
Five prey types (mammal, reptiles [2], amphibian, and bird) were used for the experiment: laboratory mice (*M. musculus*, body mass = 30 g ca.), blue-tongue skinks (*Tiliqua occipitalis*, 41 g, hereafter BT skinks), common skinks (*Ctenotus fallens*, 15 g, hereafter C skinks), frogs (*L. moorei*, 16 g), and domestic chicks (*Galus domesticus*, ca. 35 g, hereafter chicken) (Figure 1a). BT skinks do not occur on either Carnac Island or Herdsman Lake but are closely related to *E. kingii*, which is abundant on Carnac Island. The C skink *C. fallens* is commonly found on Herdsman Lake but not on Carnac Island; however, a closely related species (*Morethia obscurus*) does occur on Carnac Island.

Due to the protected status of the silver gull, it was not possible to use a live silver gull chick for the experiment, so we chose chickens as a substitute. Adult Carnac Island snakes readily feed on chickens in captivity (F Aubret, personal observation). All substitute prey (*T. occipitalis*, *C. fallens*, and *G. domesticus*) were selected based on their similarity in size and shape to the natural prey. A clean empty strainer served as control.

Ethical note. This study was approved and supervised by the Animal Ethics Committee of the University of Western Australia (Project nr 01/100/177). All procedures complied with the Animal Behavior Society/Association for the Study of Animal Behavior Guidelines for the Treatment of Animals in Behavioral Research.

Results
The number of tongue flicks directed at the strainer (the tongue flick scores) was strongly correlated with the time spent by snakes tongue flicking on the strainer for each of the 5 prey items as well as the control (Spearman ranks correlations, $35 < N < 55$, $0.96 < r < 0.98$, all $P < 0.0001$).

Within each population. Results of tongue flick scores within each population of tiger snakes are presented in Figure 2 and time scores in Figure 3. We found a significant effect of prey item on tongue flick scores in Carnac Island snakes (Friedman $\chi^2_{27,5} = 56.36$, $P < 0.001$) and in Herdsman Lake snakes ($\chi^2_{28,5} = 32.07$, $P < 0.00001$) as well as on time scores in Carnac Island snakes ($\chi^2_{27,5} = 53.57$, $P < 0.00001$) and Herdsman Lake snakes ($\chi^2_{28,5} = 24.68$, $P < 0.00016$). Statistical results are presented in Tables 2 and 3. In both populations, the mouse and frog were the preferred prey items in both tongue

Table 2
Comparison of tongue flick scores in adult tiger snakes for each pair of the 6 stimuli

Stimuli	Carnac Island					Herdsman Lake				
	Mouse	Frog	Chicken	BT skink	C skink	Mouse	Frog	Chicken	BT skink	C skink
Frog	0.201					0.943				
Chicken	0.002	0.052				0.133	0.138			
BT skink	0.001	0.001	0.085			0.001	0.001	0.063		
C skink	0.001	0.001	0.096	0.875		0.003	0.004	0.128	0.663	
Control	0.001	0.001	0.019	0.480	0.419	0.001	0.001	0.014	0.495	0.295

Data are *P* values obtained with Duncan's new multiple range test.

Table 3

Comparison of time scores in adult tiger snakes for each pair of the 6 stimuli

Stimuli	Carnac Island					Herdsman Lake				
	Mouse	Frog	Chicken	BT skink	C skink	Mouse	Frog	Chicken	BT skink	C skink
Frog	0.239					0.927				
Chicken	0.002	0.037				0.228	0.233			
BT skink	0.001	0.001	0.133			0.006	0.006	0.106		
C skink	0.001	0.001	0.099	0.808		0.011	0.012	0.149	0.787	
Control	0.001	0.001	0.036	0.470	0.596	0.001	0.001	0.038	0.591	0.451

Data are P values obtained with Duncan's new multiple range test.

flick scores and time scores. The chicken triggered the third highest tongue flick and time scores but was not statistically different from the 2 skink samples.

Between the 2 populations. A repeated-measures ANOVA with population as factor and LN "tongue flick scores" for the 6 different stimuli as the repeated measure yielded Wilks's lambda = 0.68, $P < 0.004$. There was no significant overall difference in tongue flick scores between the 2 populations for the various stimuli (interaction term: $F_{5,265} = 0.31$, $P = 0.91$, Figure 2). The various stimuli elicited significantly different tongue flick scores (effect of stimuli: $F_{5,265} = 22.51$, $P < 0.0001$). The overall level of responsiveness differed between the 2 populations (effect of population: $F_{1,53} = 18.60$, $P < 0.0001$). For instance, tongue flick scores for the control averaged 13.37 ± 11.45 in Carnac Island versus 6.21 ± 6.46 in Herdsman Lake snakes ($F_{1,53} = 6.16$, $P < 0.016$).

Similar results were obtained with time scores (Figure 3): same-design ANOVA with LN "time scores" for the 6 different stimuli as the repeated measure; Wilks's lambda = 0.67, $P < 0.003$; interaction term: $F_{5,265} = 0.47$, $P = 0.80$; effect of stimuli: $F_{5,265} = 17.68$, $P < 0.0001$; effect of population: $F_{1,53} = 19.28$, $P < 0.0001$. Time scores for control averaged 16.15 ± 11.62 in Carnac Island versus 9.14 ± 8.64 in Herdsman Lake snakes ($F_{1,53} = 6.46$, $P < 0.014$).

To account for different level of responsiveness between the 2 populations, we used a repeated-measures ANOVA design (see Methods). Statistical results are presented in Table 4. There were no significant differences between the 2 populations in the average interest shown toward the various prey items.

A few snakes attempted to bite the prey under the strainer. Of the 7 bites recorded, 3 were induced by mice and 4 by frog. All were by 6 different Herdsman Lake snakes, except for one Carnac Island snake that attempted a bite at a mouse.

Experiment 2. Tests on adult snakes with a choice of prey

We used a similar experimental design as in the single-prey tests but this time used 2 strainers, placed at equal radial distance from the first compartment (Figure 1b). Different prey items were placed under each strainer. At this stage of the study, preliminary results showed that adults from both populations were most reactive toward 3 prey types. Thus, only 3 pairings of stimuli were tested: mouse versus frog, mouse versus chicken, and chicken versus frog. We recorded the number of approaches to each strainer/prey, and the time spent tongue flicking at them. Tongue flick scores were not recorded as this was investigated in experiment 1 and both scores were highly correlated.

Results

In the Carnac Island as well as Herdsman Lake snakes, there was no significant preference in any pair of prey in the time spent tongue flicking at each prey and the number of visits to each prey (Table 5).

Feeding preferences in neonates and juveniles

Subjects and maintenance

Between 17 March 2002 and 18 May 2002, 13 wild-caught females gave birth in the laboratory (9 from Herdsman Lake and 4 from Carnac Island). Litter size averaged 5.8 ± 3.7 in Herdsman Lake females and 7.7 ± 7.5 in Carnac Island females. All females were maintained individually in plastic boxes ($50 \times 40 \times 30$ cm) with shelter, paper towel, and water dish in a controlled temperature room, at 27.5 °C by day and 20 °C by night. A heat source provided basking opportunity 4 times per day, 15 min each (high-pressure Na+ lamp, 600 W). Food (dead mice) was offered approximately every 3 weeks

Table 4

Comparison of scores with a single prey between adult tiger snakes from Carnac Island and Herdsman Lake

Stimuli	Tongue flick scores				Time scores			
	Wilks's lambda	P	df; F	P	Wilks's lambda	P	df; F	P
Mouse	0.75	0.001	1,53; 1.46	0.24	0.77	0.001	1,53; 2.54	0.12
Frog	0.88	0.035	1,53; 0.09	0.77	0.90	0.067	1,53; 0.88	0.36
Chicken	0.86	0.020	1,53; 0.05	0.83	0.91	0.072	1,53; 0.17	0.69
BT skink	0.82	0.006	1,53; 0.45	0.51	0.87	0.024	1,53; 0.70	0.41
C skink	0.82	0.006	1,53; 0.23	0.63	0.87	0.026	1,53; 0.42	0.52

Probability values are interaction terms obtained using repeated-measures ANOVA with population as factor, LN (control score) as the first measure, and LN (stimulus score) as the second measure.
df, degrees of freedom.

Table 5

Time scores and number of approaches of each prey in the choice tests in adult tiger snakes

Test	Chicken	Mouse	Frog	
Carnac Island				
Chicken versus mouse	$N = 25$			
Time (s)	48.96 ± 60.63	36.96 ± 51.92	—	$Z = 0.22, P = 0.83$
N approaches	1.32 ± 0.90	1.40 ± 1.22	—	$Z = 0.94, P = 0.36$
Frog versus chicken	$N = 25$			
Time (s)	34.24 ± 38.85	—	45.60 ± 50.98	$Z = 0.57, P = 0.56$
N approaches	1.12 ± 1.09	—	1.32 ± 0.80	$Z = 1.32, P = 0.18$
Frog versus mouse	$N = 26$			
Time (s)	—	44.77 ± 46.79	45.54 ± 59.93	$Z = 0.42, P = 0.67$
N approaches	—	1.73 ± 1.31	1.34 ± 1.26	$Z = 0.02, P = 0.98$
Herdsman Lake				
Chicken versus mouse	$N = 23$			
Time (s)	21.93 ± 15.01	15.00 ± 14.43	—	$Z = 0.76, P = 0.44$
N approaches	2.36 ± 1.45	1.44 ± 1.81	—	$Z = 0.06, P = 0.95$
Frog versus chicken	$N = 19$			
Time (s)	22.25 ± 27.33	—	12.64 ± 12.08	$Z = 0.15, P = 0.87$
N approaches	1.25 ± 0.71	—	1.73 ± 1.55	$Z = 0.28, P = 0.77$
Frog versus mouse	$N = 26$			
Time (s)	—	42.85 ± 54.48	13.54 ± 24.75	$Z = 0.79, P = 0.43$
N approaches	—	2.00 ± 1.35	0.84 ± 0.80	$Z = 1.04, P = 0.29$

Values are means ± standard deviation. Probability values are given by Wilcoxon matched-pairs tests.

and water provided ad libitum. Neonates were weighed, sexed, and measured soon after birth (Table 1) and housed in individual plastic boxes (20 × 10 × 5cm) with water dish, shelter, and paper towel substrate.

Experimental design
Individuals were never allowed to eat the prey stimulus. Each prey stimulus was presented hooked at the end of a 30-cm-long chopstick, the observer moving very little to minimize disturbance. Each prey stimulus consisted of a piece of flesh and skin of mouse (*M. musculus*), frog (*L. moorei*), C skink (*C. fallens*), wedge-tailed shearwater (*P. pacificus*), chicken (*G. domesticus*), or silver gull (*L. novaehollandiae*). No animals were specifically killed for this study. Food portions were similarly sized (ca. 10 × 5 mm) and at ambient temperature. The control stimulus was an equivalent-sized piece of white plastic. Each stimulus was slowly introduced 1 cm in front of the snake's snout, without making any direct contact. The first tongue flick directed at the stimulus began a 60-s trial where we recorded the number of tongue flicks elicited. If the snake attacked the piece of food, the latency of the attack was recorded and the test ended.

Experiment 3. Tests on neonate snakes
Tests began when neonates were 3 weeks old, allowing for behavioral maturation and depletion of yolk sacs. A total of 528 tests were performed: 209 on 31 Carnac Island neonates and 319 on 51 Herdsman Lake neonates. Snakes were tested on a 7-day schedule (for 7 different stimuli).

Results
  Within each population. Because several litters of neonates were tested for each population, we used a nested ANOVA design to account for replicate litter and potential maternal effects, with prey items as the factor, litter nested into prey items, and LN (TFASs) as the variable.
  Within Carnac Island neonates, there was a significant effect of prey on TFASs ($F_{6,178} = 11.13$, $P < 0.0001$, see Figure 4).

The results of the multiple comparisons are presented in the Table 6. All prey samples elicited similar TFASs. However, mouse samples triggered significantly lower TFASs than any other samples (other than control).
  Within Herdsman Lake neonates, we also observed an overall significant difference ($F_{6,264} = 14.68$, $P < 0.0001$). All prey samples elicited similar TFASs. Nevertheless, gull samples elicited significantly lower TFASs than any other items (other than control).
  Between populations. For the comparison between populations, we used a nested ANOVA design; nesting litter into population, population as a factor, and LN (TFAS) as the variable. The tongue flick attack for the white plastic control significantly differed between the 2 populations ($F_{1,68} = 4.12$, $P < 0.0463$), indicating a significantly different level of responsiveness among snakes in the 2 populations. Carnac Island neonates scored an average of 18.84 ± 13.97 TFAS versus
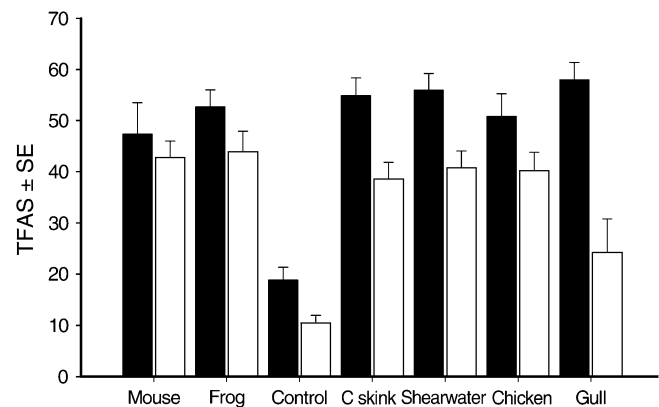
Figure 4
Graph represents TFASs ± standard error in neonate tiger snakes from Carnac Island ($N = 31$, filled bars) and Herdsman Lake ($N = 51$, open bars).

Table 6

Comparison of TFASs in neonate tiger snakes for 7 different stimuli

Stimuli	Carnac Island						Herdsman Lake					
	Chicken	Shearwater	Mouse	C skink	Gull	Frog	Chicken	Shearwater	Mouse	C skink	Gull	Frog
Shearwater	0.378						0.654					
Mouse	0.018	0.001					0.740	0.884				
C skink	0.208	0.634	0.001				0.868	0.562	0.641			
Gull	0.318	0.853	0.001	0.744			0.001	0.001	0.001	0.001		
Frog	0.748	0.259	0.031	0.129	0.210		0.983	0.654	0.737	0.861	0.001	
Control	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.004	0.001

Data are P values obtained with Duncan's new multiple range test.

10.45 ± 10.76 in Herdsman Lake neonates. If we compare the TFAS between Carnac Island and Herdsman Lake neonates (repeated-measures nested ANOVA with population as factor, litter nested into population, and LN [TFAS] of control) and each of the score for the various prey items is examined as the second repeated measure, the following statistical interactions emerged: mouse ($F_{1,68} = 0.69$, $P = 0.41$), frog ($F_{1,68} = 0.79$, $P = 0.38$), C skink ($F_{1,68} = 0.64$, $P = 0.43$), shearwater ($F_{1,68} = 0.68$, $P = 0.41$), chicken ($F_{1,68} = 0.76$, $P = 0.39$), and gull ($F_{1,33} = 6.34$, $P < 0.017$). Only the response to the gull sample differed significantly between the 2 populations.

Bites on prey. No attacks were directed at the control stimuli. All prey samples elicited some attacks by animals from both populations. We did not find any significant difference in proportions of bites among prey items in Carnac Island neonates (Pearson $\chi^2_{Dl=5} = 8.69$, $P < 0.12$, Figure 5) or in Herdsman Lake neonates ($\chi^2_{Dl=5} = 2.79$, $P = 0.73$).

Between the 2 populations (see Figure 5), the frequency of bites were not different for any items presented (Yates corrected χ^2 tests, all $P > 0.17$), although Herdsman Lake snakes bit the mouse prey most and at twice the rate of Carnac Island snakes. We found no overall difference in attack latency between Carnac Island and Herdsman Lake neonates (all tests pooled, nested ANOVA with litter nested into population; respectively, 37.60 ± 24.06 vs. 24.18 ± 19.46, $F_{1,47} = 0.19$, $P = 0.67$).

Experiment 4. Tests on juvenile snakes fed with mice
A total of 15 Carnac Island neonates were kept in the laboratory and only fed baby mice until they were 8 months of age
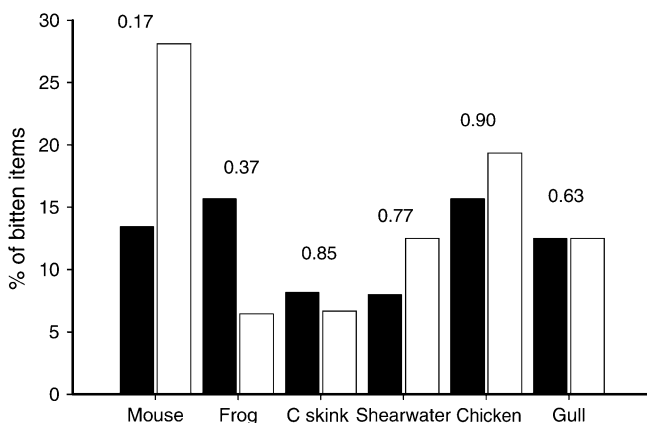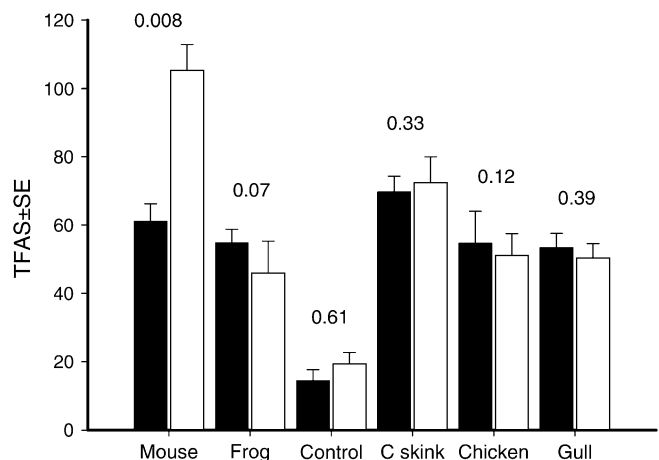
(208 ± 1.78 days of age). They averaged 17.38 ± 5.61 g in body mass and 27.96 ± 2.70 cm in snout–vent length when tested using the same prey samples as in experiment 3, with the exception of the shearwater that was not available at this time. Again, testing order was balanced (see Methods).

Results
At 8 months of age, we found a significant difference in TFASs among the different items in Carnac Island neonates (nested ANOVA with litter nested into prey item and LN [TFAS] as the variable, $F_{5,72} = 15.37$, $P < 0.0001$, Figure 6). A Duncan's new multiple range test showed that scores to mouse were significantly higher than any other items except the C skink, which came second in rates of interest (Table 7).

TFASs at 6 weeks and 8 months were compared using Wilcoxon matched-pairs tests (see Figure 6). Statistical analysis showed the greatest change in response to the mouse ($N = 15$, $Z = 2.67$, $P < 0.008$), whereas no other comparisons were significant (see Figure 6).

Occurrence of bites. Given that 15 young snakes were only fed mice throughout the experimental period, the comparison of the frequencies of bites to prey samples at 3 weeks and 8 months of age should reveal whether the initial responses of naive neonates is influenced by dietary experience. Indeed, the proportion of mouse samples bitten significantly increased from 20% to 80% (Yates corrected $\chi^2_{df=1} = 8.53$, $P < 0.004$). Frequency of bites on frog, chicken, or gull did not change significantly throughout the ontogeny (all $P > 0.10$).

Figure 5
Graph represents the proportions of bitten items in Carnac Island (filled bars) and Herdsman Lake (open bars) neonates at 3 weeks of age. Twenty-six attacks were recorded in Carnac Island neonates and 33 in Herdsman Lake. P values obtained with Yates corrected χ^2 tests for each sample between the 2 populations are given.

Figure 6
Graph represents the comparisons of TFASs ± standard error at 3 weeks (filled bars) and 8 months (open bars) of age in 15 Carnac Island neonates. The difference was significant with the mouse (Wilcoxon matched-pairs tests: $N = 15$, $Z = 2.67$, $P < 0.008$) but not for any other items. P values are given.

Table 7

Comparisons of TFASs in 15 Carnac Island neonates aged 8 months fed exclusively with mice

Stimuli	Carnac Island				
	Gull	C skink	Mouse	Frog	Chicken
C skink	0.108				
Mouse	0.001	0.066			
Frog	0.147	0.004	0.001		
Chicken	0.822	0.084	0.001	0.189	
Control	0.001	0.001	0.001	0.001	0.001

Data are *P* values obtained with Duncan's new multiple range test.

Surprisingly however, frequencies of bites on C skink also significantly increased from 0% to 43% (Yates corrected $\chi^2_{df=1} = 5.30$, $P < 0.021$).

DISCUSSION

Animals can behaviorally adapt to changes in the habitat and prey resources by adapting genetically, by individual phenotypic plasticity, or by an interaction of both processes. In widespread species, local adaptation is possible (Brodie and Garland 1993; Burghardt 1993; Burghardt and Schwartz 1999). However, gene flow may be considerable between contiguous populations and thus counteract selection for differences between populations (Krause and Burghardt 2001). Between island and mainland populations, however, gene flow may be considered as nil, unless the particular animals are capable of flying or swimming. Therefore, it is likely that genetic differences arise as 2 populations become geographically isolated. Where prey types differ, for instance, genetically based preferences may arise (Arnold 1981c, 1992; Brodie and Garland 1993; Burghardt 1993; Cooper et al. 2000).

Despite the fact that diets vary greatly between the 2 habitats, little divergence was found between the 2 populations of adult tiger snakes in the scores to different prey. Notably, adults from both locations exhibited similar interest to the various prey items offered. Unexpectedly, there were marked preferences for mouse, frog, and, to a lesser extent, chicken in both populations. These results appear counterintuitive as early dietary experience has proved to influence prey preferences in some, although not all, species of snakes (Burghardt 1967, 1969; Mori 1996; Burghardt and Krause 1999; Krause and Burghardt 2001).

Neonates responded to all prey stimuli more than to white plastic control stimuli, although there was little difference among the prey samples offered within Carnac Island and within Herdsman Lake in TFASs or in rates of bites. Moreover, the rate of biting was similar between the 2 populations for the prey sampled, as well as the TFASs for all prey samples but silver gull. Carnac Island neonates did display significantly greater TFASs toward silver gull samples than did Herdsman Lake neonates. In spite of the fact that these 2 populations (Herdsman Lake and Carnac Island) are genetically very close to one another, this result suggests that some degree of genetic and behavioral divergence exists for response to this novel prey. Previous work identified divergence for genetically fixed morphological traits between Herdsman Lake and Carnac Island populations (i.e., scalation—Aubret, Bonnet, et al. 2004).

The common mouse was one of the items preferred by adults and is commonly eaten by snakes in both populations. However, frogs do not and have never occurred on Carnac Island as there are no freshwater bodies on the island. Never-

theless, Carnac Island snakes (adults and neonates) responded to frog stimulus (a typical prey of Herdsman Lake snakes). Such behavior is probably sustained by genetic bases. Several studies showed an apparent decoupling in prey preference between 2 geographically separated populations of snakes (Burghardt 1967, 1969; Burghardt et al. 2000; Tanaka et al. 2001). This may reveal ancestral genetically fixed responses to a particular prey that is no longer consumed naturally. This is highlighted in our study, with Carnac Island snakes readily recognizing frogs as a potential prey.

A recent study has shown that in many aspects, Carnac Island represents a very favorable environment for tiger snakes (Bonnet et al. 2002): food is abundant and snakes grow to be larger than in Herdsman Lake. This fits the prediction that behavioral characters are sometimes retained for long periods under relaxed selection (for review, see Coss 1999). Interestingly, it also shows that genetically based preferences are sustained throughout ontogeny, even if the stimulus (i.e., frogs on Carnac Island) is never encountered. This may provide a selective advantage in variable environments and may account for the very large area of distribution of tiger snakes in Australia and their success in many island situations where uncommon prey occur and common prey are no longer available (typically offshore islands; Shine 1977, 1987).

On the other hand, shearwater and silver gull (and the chicken) are bird species that are never consumed by Herdsman Lake snakes as they do not nest around this lake. Despite this, Herdsman Lake neonates displayed interest in these prey items. For instance, the 3 bird species were bitten at similar rates by Herdsman Lake neonates as by Carnac Island neonates. Such behavioral flexibility may also be an advantage in variable environments, especially when populations have become isolated on islands with the rise in sea level that occurred in the past. Indeed, several tiger snake island populations have been described where nesting marine birds are a major component of the diet (Shine 1977, 1987; Schwaner 1985).

Although snakes from both populations responded similarly as both neonates and adults (no influence of dietary experience was observed), the potential for behavioral plasticity was revealed by comparing the feeding preferences of naive neonates and laboratory-reared juveniles. Previous work highlighted the potential for behavioral plasticity in these 2 populations (Bonnet et al. 2004). Carnac Island neonates raised exclusively on mice tended to increase their response to mouse stimuli even though the response at birth was already very high (in both TFASs and bite rates). That is, a strong preference for mice arose as a result of a specific diet. Unexpectedly however, skink samples triggered significantly more bites at 8 months of age rather than at 3 weeks of age, although TFASs were similar. The fact that experience on one prey type may be linked to heritable experiential effects to prey not experienced at all has been documented in gartersnakes (Burghardt et al. 2000). These results also highlight the importance in behavioral studies of comparing captive-trained animals and field-experienced animals as the results may diverge.

This study supports the value of studying recently separated populations with differing available resources as a means to explore the microevolutionary and plastic responses that populations use to adapt to environments in the early stages of genetic isolation. First, this study provides a clear example of relaxed selection on prey preference traits in a snake invading a novel environment (Coss 1999) through the retention of ancestral behavioral characters. Second, this study also provides an example of rapid selection for responsiveness toward silver gulls in Carnac Island neonates. This result is extremely interesting considering that silver gulls are the main prey of

adult snakes on Carnac Island, although never actually eaten by neonates. A recent study suggested that Carnac Island snakes have been selected at 2 levels in the process of colonizing Carnac Island (Aubret, Shine, and Bonnet 2004). Silver gull chicks are larger than the prey usually consumed by mainland conspecifics (Aubret, Bonnet, et al. 2004; Aubret, Shine, and Bonnet 2004). Carnac Island snakes (neonates and adults) not only have relatively larger heads (independent of body size) as compared with Herdsman Lake snakes but also are capable of displaying greater plasticity in head size development than Herdsman Lake individuals. Both adaptations are thought to enable ingestion of large prey and hence constitute a selective advantage in snakes that display them (Forsman 1991; Shine 1991; Forsman and Lindell 1993; Forsman and Shine 1997). The present study, therefore, relates a striking example of directional evolution in tiger snakes: a taste for a novel prey was selected concurrently with the means of ingesting it. Such linkages may also include differential growth on different diets (Burghardt et al. 2000).

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