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The influence of dehydration on the thermal preferences of the Western tiger snake, *Notechis scutatus*

Abstract Temperature selection in tiger snakes (*Notechis scutatus*) is strongly influenced by hydration state and this response varies between two distinct neighbouring populations on semi-arid Carnac Island and mainland wetland (Herdsman Lake). Fed and hydrated (control) Carnac Island snakes selected a preferred body temperature of 26.2 ± 1.2 °C and an average maximum temperature of 32.5 ± 0.5 °C in a photo-thermal gradient. Dehydrated Carnac Island snakes selected a significantly lower preferred body temperature (19.7 ± 1.6 °C) and average maximum temperature (27.7 ± 1.0 °C). Control Herdsman Lake snakes selected a preferred body temperature of 27.5 ± 0.6 °C and an average maximum temperature of 33.3 ± 0.4 °C. Dehydrated Herdsman Lake snakes selected a significantly lower preferred body temperature (23.3 ± 1.1 °C) and a lower average maximum temperature (31.8 ± 0.6 °C). Thermal depression (decreased preferred body and average maximum temperatures) in response to dehydration was greater for Carnac Island than Herdsman Lake snakes. As decreases in temperature and activity can reduce water loss, our laboratory data suggest that the survival of the relict population of tiger snakes on Carnac Island is associated with thermoregulatory modifications, which may have the effect of enhancing water conservation in this waterless habitat.

Keywords Arid · Dehydration · Reptile · Thermoregulation · Water

Abbreviations *AMT* average maximum temperature · *ATR* activity temperature range · *BCI* body condition indices · *BM* body mass · *%BML* percentage of body mass lost · *CI* Carnac Island · *EWL* evaporative water loss · *HL* Herdsman Lake · *LPBT* lower preferred body temperature · *PBT* preferred body temperature · *SVL* snout-vent length · *UPBT* upper preferred body temperature

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Introduction

Economical use of water by vertebrates is essential for survival in arid environments (Downs and Perrin 1990; Bradshaw et al. 2001). The main avenues of water loss in vertebrates are evaporative water loss (EWL) via respiration, cutaneous EWL and water lost in faeces and urine. The rate at which water is lost is strongly dependent on temperature (Mautz 1980, 1982) and activity (Nagy 1972, 1973; Minnich 1977). Most reptiles, including large elapids such as the tiger snake (Shine 1979; Schwaner 1989), actively thermoregulate, basking and shuttling between sun and shade to achieve and maintain their preferred body temperature (PBT). However, the pursuit of thermal optima is accompanied by a trade-off with potential water loss. Thermoregulation increases exposure to heat and dry air, and increases metabolic rate (Christian and Bedford 1995; Krawchuk and Brooks 1998), thereby increasing rates of cutaneous EWL (Sinsch 1989; Lillywhite et al. 1998) and respiratory water loss (Withers and Thompson 2000), the sum of which may be considerable. That hydration state may influence thermal preference has been well documented in amphibians (Preest and Pough 1989; Malvin and Woods 1991; O'Connor and Tracy 1992), but direct evidence is lacking for a similar relationship among reptiles (Ballinger et al. 1970; Huey and Slatkin 1976). If reptiles select for lower body temperature when they are dehydrated this may aid water conservation in semi-arid environments.

The degree to which ectotherms thermoregulate is dependent on a cost-benefit thermoregulation regime (Huey and Slatkin 1976). When costs are high, thermoregulation should be precise. Therefore, thermoregulation and water

balance in arid-adapted reptiles should be intrinsically linked. However, a wide range of other life-history traits also governs thermoregulation. These include reproductive status (Charland and Gregory 1990; Gregory et al. 1999; M.T. Ladyman, X. Bonnet, O. Lourdais, S.D. Bradshaw, G. Naulleau unpublished data), food intake (Saint Girons and Bradshaw 1981; Shine and Lambeck 1990), microhabitat (Robertson and Weatherhead 1992), season (Shine and Lambeck 1990; Christian and Bedford 1995), environment (Schmidt-Nielsen and Dawson 1964; Templeton 1970; Huey 1982), phylogeny (Gregory and Weatherhead 2000), morphology (Slip and Shine 1988), and competition for time allocation to life history traits (Gregory et al. 1999). Hence, thermoregulatory behaviour should be a trade-off among all these activities.

Costs associated with the maintenance of water balance in arid environments should dictate that arid-inhabiting reptiles select temperatures precisely based on their hydration state. The aim of this investigation was to test the hypothesis that hydration state strongly influences temperature selection in a reptile confined to an environment lacking free water compared with environments in which water is readily available. To achieve this we compared western tiger snakes, *Notechis scutatus*, collected from two distinct (i.e., semi-arid vs. wetland) neighbouring populations in the south west of Australia. Although described as a swamp inhabitant, tiger snakes exist on many semi-arid offshore islands throughout their range. The two Western Australian populations we investigated (Carnac Island and Herdsman Lake) have been intensively studied in recent years, which allowed us to interpret our laboratory data in an ecological context (Bonnet et al. 1999, 2002). Furthermore, field thermoregulation and thermoregulation in the laboratory has previously been documented in conspecifics and congeners (Shine 1979; Lillywhite 1980; Schwaner 1989). Therefore, temperature selection is an appropriate tool to assess the relationship between hydration state and behavioural modifications for water conservation. Our hypothesis was that dehydration results in a lower PBT and average maximum body temperature (AMT) for snakes from both populations. Our data show that the effect is greater in the semi-arid than in the wetland population, suggesting that thermal depression is an effective means of water conservation for snakes inhabiting semi-arid environments.

Materials and methods

Study site and species

Western tiger snakes (*Notechis scutatus*) used in this study were collected from Herdsman Lake (HL; 31°55′ S; 115°48′ E) and Carnac Island (CI; 32°07′ S; 115°39′ E) in the south west of Australia. Herdsman Lake is a large (400 ha) perennial freshwater lake and Carnac Island is a semi-arid near-shore (5 km) island with no free water.

Descriptive statistics

CI snakes were both heavier ($F_{1,32} = 17.39$, $P < 0.001$) and longer ($F_{1,32} = 27.75$, $P < 0.0001$) than HL snakes. The average body mass (BM) was 420.1 ± 38.5 g ($n = 16$) and 248.5 ± 18.3 g ($n = 18$) for CI and HL snakes, respectively. Snout-vent length (SVL) for CI snakes was 92.6 ± 2.1 cm ($n = 16$) while HL snakes averaged 78.8 ± 1.6 cm ($n = 18$). There was no difference in body condition indices (residuals of the $Log_{10}BM/Log_{10}SVL$ regression) between the two populations ($F_{1,31} = 1.08$, $P = 0.307$).

Conditioning regime

Snakes were held in a temperature-controlled room set on a 12-h day/night cycle with day = 28 °C and night = 15 °C. Each snake was caged individually, given water ad libitum and offered mice at weekly intervals prior to the commencement of conditioning. Snakes were fasted for a minimum of 4 days prior to testing. Only adult and sub-adult male snakes were tested and size was factored into analyses.

To determine if tiger snakes may experience dehydration in the field, morphometric and physiological data were recorded from CI snakes collected in the field over autumn, spring and summer, and these data were compared across seasons.

During conditioning, the control HL ($n = 9$) and CI ($n = 10$) snakes were maintained on the same ad libitum regime of food and water. We did not exclude food during the conditioning period, as preformed water in food may be an important water source for the snakes. Dehydrated HL ($n = 9$) and CI ($n = 6$) snakes were denied access to food and water for a period of time sufficient to reduce their body mass by greater than 10% (see Rice 1982 and Dupré and Crawford 1985 for similar methods used on lizards). As rates of dehydration vary between individuals, it was not possible to standardise the dehydration period to result in an equal percentage loss of body mass (% BML) for all individuals. HL snakes were dehydrated for an average of 44 days and CI snakes for 42 days.

Dehydration was confirmed by analysis of plasma sodium concentrations. Blood samples were taken from all snakes via cardiac puncture upon completion of thermoregulation. Samples were centrifuged (4000 rpm) for 5 min and plasma was collected. Sodium concentrations in the plasma were measured by emission spectrometry in an IL143 flame photometer using 10-μl samples with lithium chloride as an internal standard.

Thermal gradient

A photo-thermal gradient was used to establish the effect of dehydration on temperature selection in a controlled laboratory environment. The enclosure used was made of wood (2.4 m long×0.2 m wide×0.5 m deep), with a mesh top to allow ventilation and observation of snakes. The gradient was in a temperature-controlled room set on a 12 h day/night cycle with day = 15 °C and night = 10 °C. The floor of the thermal gradient was covered with sand, enabling snakes to move freely along the length of the box. A 250-W lamp, positioned 30 cm above the substrate at one end of the gradient produced a temperature range of 50–15 °C (Fig. 1). A null model used to calibrate the gradient consisted of a copper pipe (75 cm long×25 mm diameter), painted semi-gloss black, with tight rubber stoppers fitted at each end (Bakken 1992; Webb and Shine 1998). A thermocouple was suspended 2 cm into the rear of the model to approximate cloacal temperature, and another thermocouple was taped to the outer dorsal surface to approximate skin temperature. The model was coiled into a basking posture. Fig. 1 shows that inner and outer temperatures rose at approximately the same rate, and that snakes were able to choose a range of body temperatures by selecting an appropriate distance from the heat source.

Snakes were introduced into the gradient in the morning [one full 12/12-h cycle of heating (day) and cooling (night) with the heat source activated for basking], 24 h prior to testing. To
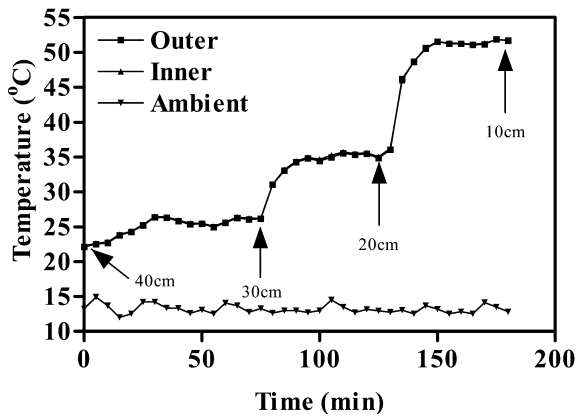
Fig. 1 Heating trace from a null model that simulated the study species. Note the lack of difference between *outer* and *inner* temperatures

minimise disturbance prior to data collection, the thermocouples (Omega) were inserted approximately 2 cm into the cloaca of the test individual, and secured with Millipore surgical tape, at least 1 h prior to activation of the heat source. The thermocouple did not restrict movement of the snakes. Output from thermocouples was fed via a switching device to a sensitive voltmeter (Thurlby) and a desktop computer converted the voltage data to degrees centigrade. Data were collected at 60-s intervals. Data were included once the snake achieved a body temperature of 20 °C (5 °C higher than room temperature) and were always collected over the same period of the day to account for diel shifts in thermoregulatory activity (Hertz et al. 1993). The minimum duration over which data were collected for a snake was 6 h following commencement of the trial.

Statistical analyses

All morphometric data are reported as mean ± SE. All data were tested for homogeneity of variance and non-homogeneous data were Log_{10} transformed prior to statistical analysis to minimise the variance (Zar 1999). $Log_{10}BM$ was used as covariates in all analyses where populations were compared, to account for the size difference between CI and HL snakes.

Body condition indices were calculated as the residuals of the $Log_{10}BM/Log_{10}SVL$ regression, and these residuals were used in some analyses. Using residual values is more appropriate than scaled values as scaled values can yield deceptive correlations due to their ratio nature (Atchley et al. 1976).

Statistical comparisons of temperatures selected by snakes were calculated using the arithmetic mean of the first 6 h temperature data (360 temperature records). The mean was chosen for ease of comparison with existing literature. However, analyses were also conducted using the median value of temperatures selected over the 6-h trial. The median is equally appropriate for analysis as it accounts for temperature selection in gradients that are negatively skewed (DeWitt and Friedman 1979). Moreover, the median is a more appropriate index for animals that thermoregulate around upper and lower body temperatures, rather than one PBT (Hertz et al. 1993). Statistics using the median are only presented when results differed from those calculated using the mean.

Upper preferred body temperature (UPBT) and lower preferred body temperature (LPBT) were established for all groups as the bounds of the temperatures recorded one standard deviation above and below the mean for each snake in each category (DeWitt and Friedman 1979). Average UPBT and LPBT were calculated as the group mean of these upper and lower temperature bounds.

Data analyses were performed using Statistica 5.1 and 6.0 (Statsoft 1995, 2001).

Results

Body condition in the field

CI snakes collected during autumn and spring were heavier, but not longer than snakes collected during summer (BM: $F_{1,39} = 6.17$, $P < 0.05$; SVL: $F_{1,39} = 1.67$, $P = 0.20$; Fig. 2a, b). Moreover, CI snakes collected during autumn had lower plasma $[Na^+]$ than snakes collected during summer ($F_{1,16} = 18.81$, $P < 0.001$) (Fig. 3). Together, these data indicated that CI snakes may suffer some degree of dehydration in the field during summer.

Effect of the conditioning regime

During conditioning the average %BML for dehydrated HL snakes was $19.2 \pm 1.8\%$ ($n = 9$; range: 12.3–29.6%), while CI snakes lost an average of $14.1 \pm 1.8\%$ ($n = 6$;
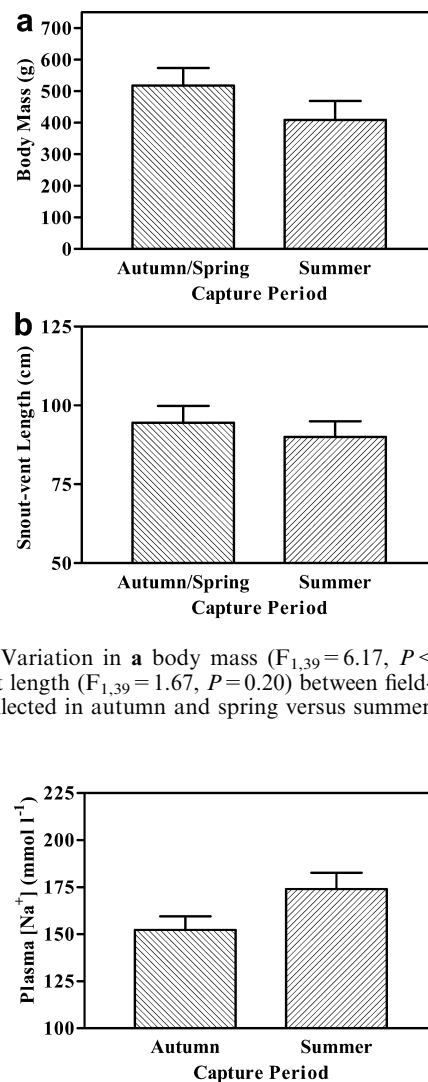
Fig. 2a–b Variation in **a** body mass ($F_{1,39} = 6.17$, $P < 0.05$) and **b** snout vent length ($F_{1,39} = 1.67$, $P = 0.20$) between field-captured CI snakes collected in autumn and spring versus summer
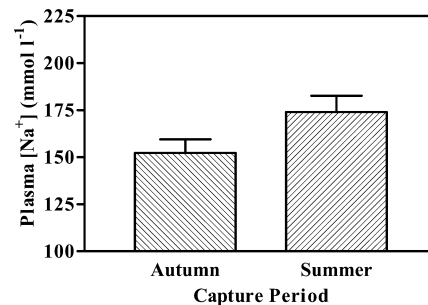

Fig. 3 Variation in plasma $[Na^+]$ between field-captured Carnac Island (CI) snakes collected in autumn versus summer

range: 10.3–22.6%). This difference was significant ($F_{1,13} = 5.08$, $P < 0.05$).

Plasma [Na^+] analysis revealed that dehydrated snakes from both populations had a higher [Na^+] than control snakes (nested ANCOVA: $F_{1,25} = 72.70$, $P < 0.001$). Plasma [Na^+] was 158.3 ± 1.6 mmol l^{-1} ($n = 8$) and 150.0 ± 3.9 mmol l^{-1} ($n = 7$) for control HL and CI snakes, respectively, while plasma [Na^+] was 200.0 ± 4.7 mmol l^{-1} ($n = 9$) and 177.6 ± 3.8 mmol l^{-1} ($n = 6$) for dehydrated HL and CI snakes, respectively. Moreover, there was a strong, positive ($r^2 = 0.65$) and highly significant ($P < 0.001$) relationship between %BML and plasma [Na^+] for all snakes (Fig. 4).

Patterns of temperature selection

Traces of temperature selection over time revealed that snakes typically engaged in a period of warming to a threshold temperature, after which they established a cycle of heating and cooling by moving toward and away from the heat source. UPBT and LPBT were calculated (see Materials and methods) and, even though these temperatures varied between populations and categories, the temperature range of 7.0 °C (UPBT minus LPBT) was not significantly different between categories (control vs. dehydrated) for both populations (HL snakes–$F_{1,17} = 0.35$, $P = 0.56$: CI snakes–$F_{1,15} = 0.30$, $P = 0.59$; Table 1). However, the temperature range selected by dehydrated CI and HL snakes was distributed around a lower mean (see following section
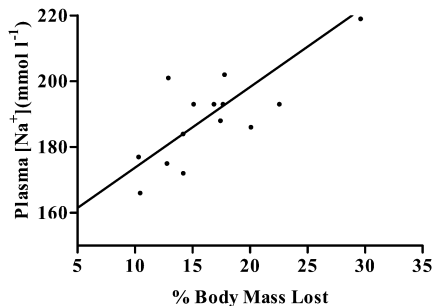
Fig. 4 Relationship between percentage body mass lost and plasma [Na^+] in all snakes subjected to the dehydration regime ($Y = 2.45X + 149.2$, $r^2 = 0.65$, $P < 0.001$, $n = 15$)

and Fig. 5a, b). Furthermore, dehydrated CI and HL snakes selected a range of temperatures that were more normally distributed than temperatures selected by control snakes that showed a strong negative skew (Table 1).

Comparisons of temperature selection

Body temperature of snakes in the thermal gradient did not exceed 35 °C, despite the fact that temperatures under the heat/light source exceeded 50 °C.
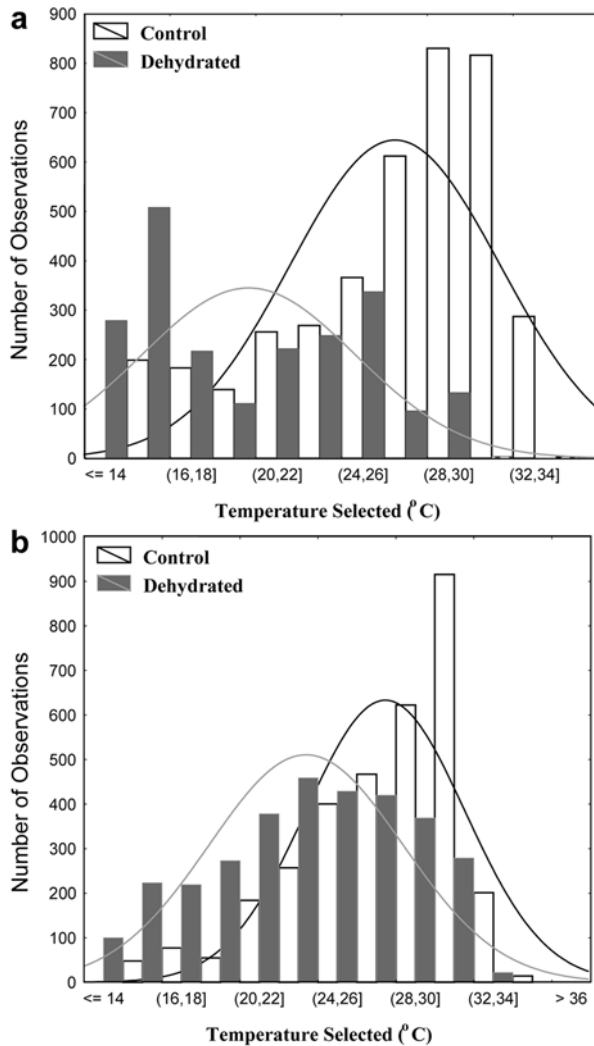
An overall comparison of the two populations revealed that CI snakes, despite being less dehydrated, selected lower PBTs and AMTs than HL snakes (nested ANCOVA: PBT: $F_{1,29} = 12.29$, $P < 0.01$; AMT: $F_{1,30} = 7.91$, $P < 0.01$; Table 2). Moreover, the decrease in temperature from control PBT and AMT to dehydrated PBT and AMT was greater for CI snakes than HL snakes. PBT and AMT decreased by 6.6 °C and 4.8 °C, respectively, for CI snakes. These temperatures decreased by only 4.2 °C and 1.4 °C, respectively, for HL snakes.

Because there was a difference between CI and HL snakes in terms of the severity of dehydration (%BML), regression analyses were performed to investigate the relationship between body condition and temperature selection (body condition indices, BCI, used in place of %BML to enable control animals to be incorporated in the data set). Regression analysis revealed that PBT increased as body condition increased for both populations (Fig. 6a: HL snakes $Y = 0.48 \pm 0.14X + 1.40 \pm 0.01$, $r^2 = 0.43$, $P < 0.01$, $n = 18$; Fig. 6b: CI snakes $Y = 1.14 \pm 0.29X + 1.37 \pm 0.02$, $r^2 = 0.53$, $P < 0.01$, $n = 16$). These data suggest that, had both HL and CI snakes been dehydrated equally the difference between the two populations would have been exacerbated.

Within the CI population, dehydrated snakes maintained a lower PBT and AMT than control snakes ($P < 0.01$, MANOVA: Wilks$_{2,13} = 0.38$; Table 2). This was not entirely the case for HL snakes. The overall result was the same ($P < 0.05$, MANOVA: Wilks$_{2,15} = 0.63$), but a subtle difference was observed; AMT was not significantly different between categories ($F_{1,16} = 3.43$, $P = 0.08$; Table 2). All results reported were consistent for both populations when the median temperature selected was used for the analyses.

	Category	Set point	Average temperature(°C)	Average temp. range (°C)	Skewness
Carnac Island	Control	UPBT ($n = 11$)	29.7 ± 0.9	6.4	−0.866
		LPBT ($n = 11$)	23.3 ± 1.4	–	–
	Dehydrated	UPBT ($n = 6$)	23.2 ± 1.7	6.9	0.272
		LPBT ($n = 6$)	16.1 ± 1.4	–	–
Herdsman Lake	Control	UPBT ($n = 10$)	30.9 ± 0.3	7.1	−0.945
		LPBT ($n = 10$)	24.0 ± 0.9	–	–
	Dehydrated	UPBT ($n = 9$)	27.0 ± 1.1	7.4	−0.2427
		LPBT ($n = 9$)	19.6 ± 1.3	–	–

Table 1 Summary of upper preferred body temperature (*UPBT*), lower preferred body temperature (*LPBT*) and skewness of temperatures recorded for Carnac Island (CI) and Herdsman Lake (HL) snakes in a thermal gradient

Fig. 5a–b Histograms of the distribution of temperatures selected by control and dehydrated Carnac Island (CI) snakes (a) and Herdsman Lake (HL) snakes (b) during a 6-h period in a thermal gradient. Data for CI snakes are an assimilation of the first 360 temperature records for 11 control and 6 dehydrated individuals, while data for HL snakes are from 9 control and 9 dehydrated individuals

Discussion

Our data show that hydration state has a marked effect on thermal preferences of the western tiger snake, with dehydrated snakes from both populations selecting lower PBTs. Our data also indicate that snakes from semi-arid CI exhibit a greater response to dehydration than wetland HL snakes; CI snakes responded to dehydration with a greater depression of PBT and AMT than HL snakes, despite being less dehydrated. In fact, HL snakes did not significantly decrease AMT in response to dehydration. We also provide evidence that CI snakes suffer some degree of seasonal dehydration in the field. As a decrease in temperature and activity can reduce water loss, these data suggest that the survival of
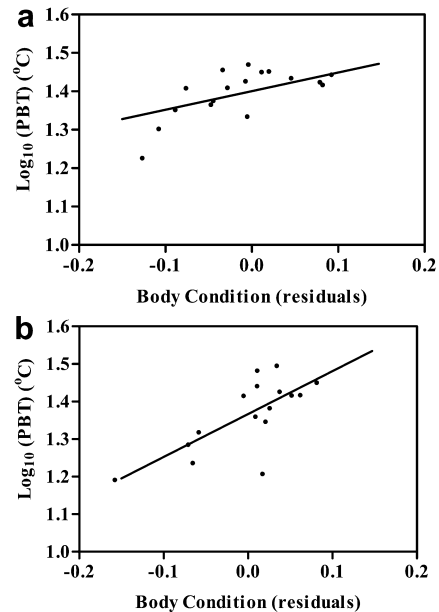
Fig. 6a–b Relationship between body condition and Log_{10} preferred body temperature (*PBT*). a HL snakes ($Y = 0.48 \pm 0.14X + 1.40 \pm 0.01$, $r^2 = 0.43$, $P < 0.01$, $n = 18$). b CI snakes ($Y = 1.14 \pm 0.29X + 1.37 \pm 0.02$, $r^2 = 0.53$, $P < 0.01$, $n = 16$)

the relict population of tiger snakes on CI is associated with thermoregulatory modifications, which may have the effect of enhancing water-conservation in this waterless habitat.

Available field (Shine 1979; Schwaner 1989) and laboratory (Lillywhite 1980) data provide evidence that tiger snakes actively regulate body temperature, giving us a foundation from which to explore temperature selection under the influence of varying hydration states. Although our data are not representative of the complexities of thermoregulation in the field, we have revealed some interesting patterns of temperature selection. However, prior to interpretation of the data it was necessary to identify the thermal characteristics of the gradient used. Our null model (an approximation of our study animal) provides evidence that animals were able to select a range of temperatures from room temperature (15 °C) to more than 50 °C. The heating curve for the null model also demonstrates that core temperature heats at a similar rate to external temperature in our system (Fig. 1). Therefore, all snakes tested were able to achieve a range of core (cloacal) temperatures by moving along the gradient without exterior (skin) surfaces becoming too hot.

Temperatures selected by our tiger snakes were consistent with laboratory data of other authors for similar and distantly related species. Lillywhite (1980) reported mean body temperatures of 32.2 ± 1.58 °C (±SD) for *Notechis scutatus* in a thermal gradient, though it is not clear from where across their range the snakes were collected, or from what habitat. Webb and Shine (1998) reported that the broad-headed snake, *Hoplocephalus bungaroides*, selects body temperatures between 28.1 °C

Table 2 Summary temperature data for snakes from the two populations presented for the two treatment groups

	Condition	Average temperature (°C)	Median temperature (°C)	Average maximum temperature (°C)	Highest temperature (°C)
Carnac Island	Control ($n = 10$)	26.2 ± 1.2	27.7 ± 1.0	32.5 ± 0.5	34.2
	Dehydrated ($n = 6$)	19.7 ± 1.6	19.2 ± 1.9	27.7 ± 1.0	28.9
Herdsman Lake	Control ($n = 9$)	27.5 ± 0.6	28.1 ± 0.7	33.3 ± 0.4	34.9
	Dehydrated ($n = 9$)	23.3 ± 1.1	23.4 ± 1.3	31.8 ± 0.6	34.9

and 31.1 °C in a thermal gradient. Our data also fall within the range of preferred field body temperatures previously documented for many snakes (27–35 °C; Duguy 1972; Lillywhite 1980, 1987; Rosen 1991; Beck 1995; Brown and Weatherhead 2000; Rohr and Malone 2001).

Patterns of temperature selection in the thermal gradient were also similar to those described by several authors for squamates (Heath 1970; Berk and Heath 1975) with snakes shuttling along a continual temperature gradient to achieve high and low body temperatures. To determine the upper and lower body temperatures selected, we calculated the bounds of the central 68% (one standard deviation above and below the mean) of the temperature records (Hertz et al. 1993) and determined a temperature range of 7 °C that was consistent across the groups tested. Acknowledging the limitations of the laboratory data, we suggest that this shuttling behaviour provides some evidence of an "activity temperature range" (Cowles and Bogert 1944) in which snakes regulate their body temperature between upper and lower set points (Berk and Heath 1975; Barber and Crawford 1977). In accordance with this, we observed that dehydration stimulated, not only a decreased PBT, but also a downward shift of UPBT and LPBT with the maintenance of the same temperature range (7 °C) for CI and HL snakes (Hertz et al. 1993). This downward shift in the range of temperatures selected may have some ecological significance. However, our interpretations are limited by the limitations of our laboratory data. We suggest that dehydration shifts the balance of the trade-off between thermoregulation and the need for daily activity to a point where both thermoregulatory behaviour and activity are reduced in favour of water conservation. In extreme cases of dehydration, activity and thermoregulation are probably abandoned, as in the case of many desert lizards (Bradshaw 1997).

Control CI and HL snakes selected a range of temperatures in the thermal gradient that were strongly negatively skewed; a typical pattern of temperature selection for reptiles in a thermal gradient (DeWitt and Friedman 1979). However, temperatures selected by dehydrated snakes were more normally distributed and the reasons for this are open to interpretation. Dehydrated CI snakes frequently selected very low temperatures and the temperature distribution was the only one of the four groups that was positively skewed (Fig. 5a). Given the origin of these animals (semi-arid), the selection of low temperatures during periods of water shortage may result in water conservation. In contrast, HL snakes (wetland origin) more frequently selected moderate temperatures, with a less obvious divergence from the control group (Fig. 5b).

The strong correlation between %BML and plasma [Na$^+$] provides evidence that our conditioning regime did, in fact, cause dehydration in these treatment groups (Fig. 4; Dessauer 1970; Bentley 1976; Minnich 1979, 1982). In addition, we observed that HL snakes dehydrated more rapidly than CI snakes. There may be several reasons for this, the most obvious of which is the effect of allometry on the rate of dehydration; smaller HL snakes lost water faster as they have a greater surface area to volume ratio. HL snakes also suffer heavy parasite loads, where CI snakes do not, which may influence respiratory water loss, and subsequent rates of dehydration (F. Aubret, unpublished data). Irrespective of the difference in the rate and severity of dehydration between HL and CI snakes, the effect of dehydration on temperature selection was clear: dehydrated snakes selected lower body temperatures than control snakes. In addition, CI snakes exhibited a more pronounced thermal depression than HL snakes, despite being less dehydrated. This response was consistent for PBT (6.6 °C for CI and 4.2 °C for HL), and AMT (4.8 °C for CI and 1.4 °C for HL). In fact, among HL snakes, AMT did not differ significantly between the two treatment groups. Arguably, the different states of dehydration may potentially confound this comparison. However, regression analysis reveals that PBT increases as body condition increases or vice versa (Fig. 6). Therefore, the differences we have revealed would have been even more pronounced had all snakes been dehydrated equally.

The different response (the extent of thermal depression) to changes in hydration state between the two populations tested strongly supports the idea that temperature selection is more precisely regulated in populations where the costs of thermoregulation may be high. It is clear that high temperatures increase evaporative water loss (Mautz 1980, 1982). Irrespective of their thermoregulatory regime, HL snakes would not pay a cost of thermoregulation in terms of water loss as they can readily rehydrate at any time. This is not the case for CI snakes; they have no access to free water over the long summer months and must normally derive all their water input from their diet and metabolic water production. Our field data on the seasonal change in BM and plasma [Na$^+$] for CI snakes provide strong evidence that these snakes may suffer some degree of dehydration over summer, and our laboratory data suggest that CI snakes have modified their thermoregulatory behaviour, with water conservation having a higher priority when

water is scarce. For CI snakes, an early response (thermal depression) to dehydration during summer may increase the likelihood of survival to the following wet season. This conclusion is further supported by low capture rates of tiger snakes on CI during the dry summer months, suggesting animals actively avoid exposure (X. Bonnet, personal communication). This type of environmental familiarity has been shown by other authors to enhance the fitness of conspecifics in variable environments. Chelazzi and Calzolai (1986) demonstrated that familiarity with microenvironment facilitates more efficient behavioural thermoregulation in the tortoise *Testudo hermanni*. In the lizard *Sceloporus undulatus*, New Mexican conspecifics in drier habitats give water conservation a higher priority than Colorado conspecifics from a wetter habitat (Crowley 1987). Whether the thermoregulatory response of tiger snakes to dehydration has a phylogenetic basis or is attributable to phenotypic plasticity remains to be tested.

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