
BEHAVIORAL THERMOREGULATION OF THE TUATARA, *SPHENODON PUNCTATUS*, UNDER HYDRIC AND DIGESTIVE CONSTRAINTS

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Abstract.—Burrow use is an important component of the behavioral repertoire of many terrestrial reptiles. The availability and/or selection of suitable burrows within the environment may have consequences for fitness as retreat site selection can affect the physiology and ecology of an animal. Thermal behavior and microhabitat selection may vary with respect to ambient temperatures, humidity levels, and the digestive state of the organism. To understand behavioral and physiological regulation mechanisms, we investigated the thermal biology of the Tuatara, *Sphenodon punctatus*, a medium-sized reptile that use underground burrows as general shelter. We gave captive, juvenile Tuatara a series of choices between burrows varying in temperature and humidity while in a fed or post-absorptive state. We did this to test hypotheses that Tuatara choose burrows based on temperature and humidity, and that those choices may change with the metabolic requirements of digestion. Tuatara selected warm temperatures regardless of digestive state, humidity, or time of the day. However, there was a clear diel trend in thermoregulatory behavior with Tuatara maintaining warmer body temperatures and using warmer parts of the gradient during the day. Tuatara were outside their burrows and moved about the thermal gradient more often during the night. Tuatara selected higher temperatures on the gradient under the dry treatment than they did in the humid treatment. However, Tuatara were outside their burrows in greater numbers under the humid treatment compared to the dry. Digestive state had no discernable effect on either temperatures selected or burrow use. This study provides experimental evidence that reptiles are capable of adjusting their habitat selection behavior in response to differing humidity constraints.

Key Words.—burrow selection; humidity; microhabitat; retreat; temperature; thermophysiology

INTRODUCTION

Detailed studies on microhabitat and microclimate are important to understand the biology and evolution of retreat site use and the adaptive significance of specific morphological, physiological, behavioral, and ecological traits (Burda et al. 2007). Physiological consequences of habitat selection are ecologically important (Huey 1991), and within a given habitat the presence of suitable retreats for a particular species has consequences for fitness. Knowledge of the criteria used for choice of burrows may elucidate the manner by which animals maintain their associations with particular microhabitats in the field. Our laboratory-based study investigated three predictors that are known to influence retreat site selection in ectotherms: temperature (Webb and Shine 1998), humidity (Schlesinger and Shine 1994), and digestive state (Blouin-Demers and Weatherhead 2001a). Laboratory studies allow the simplification of the environment of an organism, enabling discrete influences on burrow selection to be teased apart under controlled conditions, something that is not easily achievable in the field.

Temperature has a profound effect on the performance of organisms such as invertebrates and ectothermic vertebrates (Hochachka and Somero 1984;

Cossins and Bowler 1987; Angilletta et al. 2002). These organisms therefore need an effective means of coping with, or evaluating spatial and temporal heterogeneity in the thermal environment, and as a consequence, the availability of thermally suitable retreat-sites may determine patterns of habitat use by many ectotherms (Huey 1991). The body temperature of a terrestrial reptile may be lowered by the loss of heat due to evaporation of body fluids (Bogert 1949). Thus humidity can influence behavioral thermoregulation, and variation in burrow microclimate may influence retreat site selection (Bulova 2002).

The digestive state of an animal is another factor that can influence retreat site selection. Many ectothermic vertebrates maintain warmer body temperatures after feeding to increase the rate of processing, a strategy termed post-prandial thermophily (Kitchell 1969; Gatten 1974; Lang 1979; Slip and Shine 1988). For instance, Green Anoles (*Anolis carolinensis*) selected lower temperatures on a thermal gradient after food deprivation (Brown and Griffin 2005), and snakes (Texas Ratsnakes, *Elaphe obsoleta*) selected higher temperatures on a thermal gradient (Blouin-Demers and Weatherhead 2001b) and in the field (*Crotalus* sp.; Beck 1996) after feeding. During environmental conditions in which suitable

prey items are readily available, a faster rate of digestion with increased body temperatures may enable higher consumption and growth rates.

We investigated the relative importance of temperature, humidity and digestive state in retreat site selection in the Tuatara (*Sphenodon punctatus*). The Tuatara is a medium-sized, long-lived reptile (~100 y; Gaze 2001) that is endemic to New Zealand, and is the sole, extant representative of the once diverse, ancient reptilian order Rhynchocephalia (sensu Gauthier et al. 1988). Tuatara are a diurnal-nocturnal, burrowing species. They forage mainly at night when air temperatures are typically low (Walls 1983) and are active at temperatures as low as 5.2° C (Thompson and Daugherty 1998), but they also bask and feed during the day, attaining body temperatures up to 34.5° C (Ilse Corkery, unpub. data). The relatively simple spatial structure of Tuatara populations is highly stable over years, possibly decades, and they can maintain particular burrows for long periods of time (Moore et al. 2009), despite the potential availability of many other burrows. For example, on Stephens Island (also known by its Maori name *Takapourewa*), there are many more burrows than there are Tuatara, as most burrows are excavated by Fairy Prions (*Pachyptila turtur*), and there are greater numbers of seabirds than Tuatara (approximately 1,000,000:40,000).

Our study was conducted with captive juveniles only. However, the thermal environment and thermal preference of wild adults is similar to those of juveniles (Besson and Cree 2010b), and several months post-hatching, juvenile Tuatara have a similar circadian rhythm and emergence pattern to those of adults (Birchard et al. 2006). Therefore, we suggest that the results of this study are also applicable for adult Tuatara. We predicted that the Tuatara would exhibit non-random selection between alternative retreat sites in the laboratory. Specifically, we wanted to test the hypotheses that Tuatara choose burrows based on temperature and humidity, and that those choices may vary with the metabolic requirements of digestion.

MATERIALS AND METHODS

Study organisms and maintenance.—We used one-year-old juvenile Tuatara ($n = 24$) of unknown sex (as juvenile Tuatara are not obviously sexually dimorphic), with a mass between 17.1 g to 39.9 g that were incubated and raised from eggs originating from Stephens Island (Cook Strait, New Zealand; e.g., Nelson et al. 2004). At the Victoria University of Wellington, we housed groups of four to six individuals in six open-topped 60 × 70 × 35 cm metal containers containing substrate of a 20 cm deep mix of horticultural sand, bark mulch, and top soil with leaf litter. We provided a photoperiod of 12:12 LD (0700–1900) with full spectrum lights (Arcadia-D3, Arcadia, Redhill, UK) placed 75 cm above the enclosures. We dusted live crickets, mealworms, and flies with

calcium and vitamin powder and released these into the enclosures once a week. All 24 individuals were healthy and regularly took food. We provided water *ad libitum*. Because an animal's thermoregulatory behavior may be strongly influenced by the particular design of a thermal gradient (Wall and Shine 2008), we conducted this experiment in the same housing conditions within which the Tuatara were acclimated.

Experimental procedure.—Before commencing the experiment, we inserted a cloacal thermocouple (a polyethylene coated 30 gauge copper-constantan wire attached to a thermometer; Fluke® 51, Fluke Inc., Everett, Washington, USA; precision 0.05% ± 0.3° C) ~10 mm into the cloaca of three Tuatara to determine whether Tuatara internal body temperatures corresponded to external body temperatures taken with an infra-red thermometer (IRT: Raytek, Raynger® model ST80 ProPlus™, Santa Cruz, California, USA; precision 0.1° C, accuracy ± 2° C between -18 and 23° C and ± 1° C above 23° C for surfaces with an emissivity of 0.95). We assumed that the skin of Tuatara had a similar emissivity to 0.95, which appears reasonable as most biological materials have an emissivity in the medium to long infrared spectrum of between 0.90 and 0.99 (Willmer et al. 2005). We coated the tip of the temperature probe in araldite glue (Araldite® Adhesives, Huntsman Advanced Materials, Basel, Switzerland) to provide a small, smooth bulb, and calibrated the thermocouple to 0° C using an ice bath. We ensured that the IRT was orientated in line with the Tuatara's body axis to eliminate the effect of background temperature (Hare et al. 2007). Temperatures taken with the IRT were always within 0.5° C of temperatures measured with the internal thermocouple. This result was consistent with research on amphibians (Rowley and Alford 2007) and both juvenile Tuatara and small lizards (Hare et al. 2007). For example, in a previous study with Tuatara, 95% of paired temperature values using an IRT differed by no more than 1° C (Hare et al. 2007). Thus skin temperature was assumed to represent core body temperature.

We constructed 12 thermal gradients using metal containers identical to normal housing conditions for substrate and photoperiod. One end of the thermal gradient was heated from below by Nu-Klear (Nu-Klear®, Auckland, New Zealand) thermostatically controlled electric heat pads (43.5 × 35.0 cm) while the opposite end was cooled using ice packs, which we replaced as melting occurred (approximately every 3–4 h). This provided a range of temperatures over a length of 700 mm, from 8.5 to 30.5° C (± 1.0° C), which is within the range of minimum and maximum recorded body temperatures of Tuatara on Stephens Island (4.5–34.5° C, Ilse Corkery, unpub. data). We placed four, 20 cm long burrows (cardboard tubes; diameter 50 mm) at set intervals along the gradient and on top of the substrate, where air temperatures were 10, 16, 21, and 27° C (± 1.5° C), respectively. We

TABLE 1. Order of treatment for 24 Tuatara (*Sphenodon punctatus*) during feeding trials. We tested 12 animals each week, which we divided into two treatment groups.

		Group 1 (1–6)	Group 2 (7–12)	Group 3 (13–18)	Group 4 (19–24)
Week 1	Day 1 Day 2	Dry + Fed Humid + Fed	Dry + Unfed Humid + Unfed		
Week 2	Day 1 Day 2			Dry + Fed Humid + Fed	Dry + Unfed Humid + Unfed
Week 3	Day 1 Day 2	Dry + Unfed Humid + Unfed	Dry + Fed Humid + Fed		
Week 4	Day 1 Day 2			Dry + Unfed Humid + Unfed	Dry + Fed Humid + Fed

spot-checked temperatures on top of the substrate along the gradients throughout the experiment with an infra-red thermometer (IRT). We placed a filled (2 cm deep) water container (radius 3.5 cm) at the entrance to all four burrows to ensure access to water was never a factor in choice of burrow. We measured humidity with data loggers (Hobo® Onset Computer Corporation, Cape Cod, Massachusetts, USA; accuracy: RH: $\pm 3.5\%$ from 25% to 85% over the range of 15° C to 45° C) placed in the center of the first and last housing containers.

We placed individuals in the center of each thermal gradient, facing either the hot or cold end (50% each way, random placement), 24 h before the first observation occurred, to minimize the effects of stress from handling on observations and to allow exploration of the new environment. We tested all 24 animals under “Fed,” “Unfed,” “Dry,” and “Humid” treatments with 12 animals tested at one time (Table 1). The “Fed” treatment was comprised of animals fed immediately prior to the experiment while the “Unfed” treatment was made up of animals fasted for six days prior to the study to ensure they were in a post-absorptive state. Under normal husbandry conditions, we feed Tuataras once every seven days, meaning that both treatments “Fed” and “Fasted” were normal physiological states within the standard feeding regime of an individual. The “Dry” treatment was under normal conditions (35.1–51.7% RH). We soaked each enclosure with a water spray (including cardboard tubes) and misted regularly to maintain a relative humidity of 55.7–70.8% RH for the “Humid” treatment. We completed the experiments over the course of four weeks; in week one, we tested 12 animals with six “Fed” and six “Unfed.” We observed them in a dry treatment for 24 h and then in a humid treatment for 24 h. After 72 h, we returned Tuatara to their original housing conditions. In week two, we tested 12 new animals. In weeks three and four, we tested the animals from weeks one and two again but “Fed” and “Unfed” treatments were reversed to ensure that all individuals experienced all treatments (Table 1).

The thermal gradient was divided into four temperature bands: area 1, the coldest end (8.5–12 °C);

area 2 (12–19 °C); area 3 (19–26 °C); and area 4, the warmest end (26–30.5 °C). After the initial 24 h, we took observations every hour (for the next 48 h) using a small handheld mirror with a diameter of 50 mm (Tuatara were difficult to spot if they were located in the center of a burrow) and night vision goggles during hours of darkness. Observations consisted of recording the area of gradient in which the Tuatara was located, whether it was inside, outside, or on top of a burrow, and body temperature (if outside burrow) with the infra-red thermometer.

Statistical analysis.—Data were not normally distributed and included missing observations (when Tuatara were inside burrows, temperatures could not be taken and no substitute values were used). We used Generalized Estimating Equations (repeated measures generalized linear mixed models) to test for differences in body temperature, area selected on gradient, and time spent in burrows as these models do not make any distributional assumptions (Zuur et al. 2009). The predictor variables were digestive state, humidity, and time (day: 0700–1900, versus night: 2000–0600), and data were repeated across individuals, treatments, and time. Data are presented as means ± 1 SE without transformation. We analyzed data using the statistical software SPSS, version 18.0 (SPSS Inc.), and we considered *P* values ≤ 0.05 significant in all tests.

RESULTS

The order in which we tested each Tuatara (trial 1, 2, 3 or 4) had no significant effect on temperature selected (Wald $\chi^2 = 6.729$, *df* = 3, *P* = 0.081), area selected (Wald $\chi^2 = 4.202$, *df* = 3, *P* = 0.240), or burrow use (Wald $\chi^2 = 2.213$, *df* = 3, *P* = 0.529); therefore, for all subsequent analyses, we pooled data from all four trials.

Temperatures selected.—Body temperatures of juvenile Tuatara on the thermal gradient ranged from 9.6 to 27.1° C (*n* = 1,081 measurements). The mean temperature selected was 19.6 \pm 0.1° C (Interquartile Range [IQR]: 17.8–21.8° C). Both time (Wald $\chi^2 =$

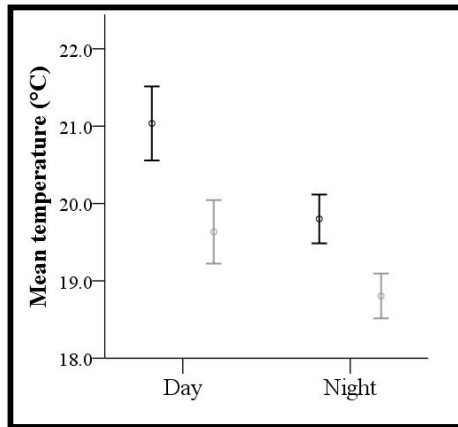


FIGURE 1. Mean selected body temperatures and 95% confidence intervals of Tuatara (*Sphenodon punctatus*) during night (2000–0600) and day (0700–1900), and under dry (black) and humid (grey) treatments.

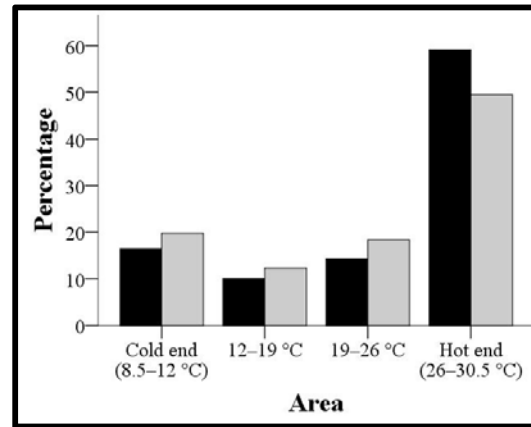


FIGURE 2. Percentage time spent by Tuataras (*Sphenodon punctatus*) in each area under dry (black bars) and humid (grey bars) treatments.

16.789, $df = 1$, $P < 0.001$) and humidity (Wald $\chi^2 = 17.460$, $df = 1$, $P < 0.001$) had significant influences on the body temperature of Tuatara, but digestive state (Wald $\chi^2 = 1.041$, $df = 1$, $P = 0.308$) did not significantly alter temperature selected, and none of the interactions were significant. Mean body temperature selected during the day ($20.3 \pm 0.1^\circ\text{C}$; IQR: $18.4\text{--}22.4^\circ\text{C}$), was significantly higher than during the night ($19.3 \pm 0.2^\circ\text{C}$; IQR: $17.4\text{--}21.4^\circ\text{C}$; Wald $\chi^2 = 16.789$, $df = 1$, $P < 0.001$; Fig. 1). We observed a higher percentage of Tuatara in area 4 (warmest end) during the night (Table 2).

The mean body temperatures in the dry treatment was $20.3 \pm 0.1^\circ\text{C}$, (IQR: $18.4\text{--}22.4^\circ\text{C}$), which was significantly higher than in the humid treatment ($19.1 \pm 0.1^\circ\text{C}$, IQR: $17.2\text{--}21.2^\circ\text{C}$, Wald $\chi^2 = 17.460$, $df = 1$, $P < 0.001$). During the dry treatment, 59.1% of all recordings were in area 4 (warmest area), with a lower percentage, (49.5%) in this area during the humid treatment (Fig. 2). Digestive state did not significantly influence body temperature (Wald $\chi^2 = 1.041$, $df = 1$, $P = 0.308$). Tuatara fed prior to the experiment had a mean body temperature of $19.6 \pm 0.2^\circ\text{C}$, while those in post-absorptive state had a mean body temperature of $20.0 \pm 0.3^\circ\text{C}$.

Burrow use.—Overall, we recorded Tuatara inside their burrows 42.6% of the time ($n = 981$

observations). Of the Tuatara that remained within their burrow for longer than one hour (for at least two consecutive observations), 78% ($n = 637$) were in the warmest area, 11.5% ($n = 93$) were in the coldest area, and the remainder were in areas 2 (3.5%) and 3 (7%). Humidity and time had significant effects on how a Tuatara used a burrow ($\beta_{\text{threshold(out. burrow)}} = 3.457$; 95% CI = $0.227\text{--}3.012$, Wald $\chi^2 = 231.13$, $P < 0.001$). We recorded significantly more Tuatara outside their burrows in humid conditions and more inside their burrow under the dry treatment (Wald $\chi^2 = 11.904$, $d.f. = 1$, $P = 0.001$), (Fig. 3). We recorded significantly fewer (Wald $\chi^2 = 25.858$, $df = 1$, $P < 0.001$) Tuatara outside their burrows during the day (Table 3). Digestive state had no influence on burrow use (Wald $\chi^2 = 0.146$, $df = 1$, $P = 0.702$; Table 3). None of the interactions were significant.

Movement on gradient.—The GEE model investigating movement on the gradient revealed that both time and humidity influenced movement. Juvenile Tuatara moved significantly more during the night than during the day (Wald $\chi^2 = 6.046$, $df = 1$, $P = 0.014$). The Tuatara also moved significantly more in the humid treatment than in the dry treatment (Wald $\chi^2 = 16.768$, $df = 1$, $P < 0.001$). Digestive state had no influence on movement (Wald $\chi^2 = 0.001$, $df = 1$, $P =$

TABLE 2. Percentage of recorded Tuatara (*Sphenodon punctatus*) in each of the four temperature bands of the gradient.

Area	1 (cold end)	2	3	4 (warm end)
Day	18.3	8.1	13.9	59.7
Night	18.0	14.9	19.2	47.9
Dry	16.5	10.1	14.3	59.1
Humid	19.8	12.3	18.4	49.5
Fed	14.3	10.8	17.6	57.3
Unfed	22.0	11.6	15.1	51.3

TABLE 3. Percentage of recorded Tuatara (*Sphenodon punctatus*) inside and outside burrows, with those on top of burrows displayed within parentheses.

Area	Inside burrow	Outside burrow
Day	68.9	31.1 (3.1)
Night	37.7	62.3 (5.1)
Dry	55.8	44.2 (4.4)
Humid	45.5	54.5 (3.8)
Fed	45.5	54.5 (4)
Unfed	52.1	47.9 (4.3)

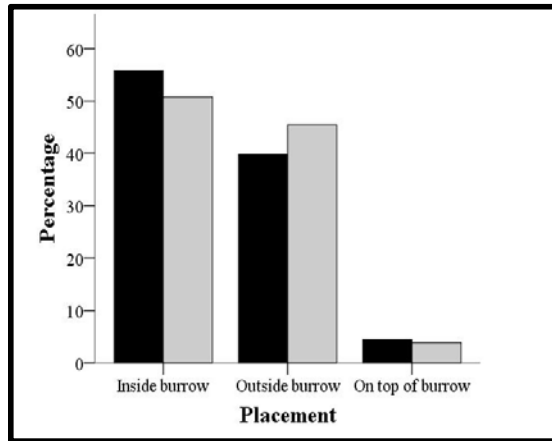


FIGURE 3. Burrow use of Tuatara (*Sphenodon punctatus*) under dry (black) and humid (grey) treatments.

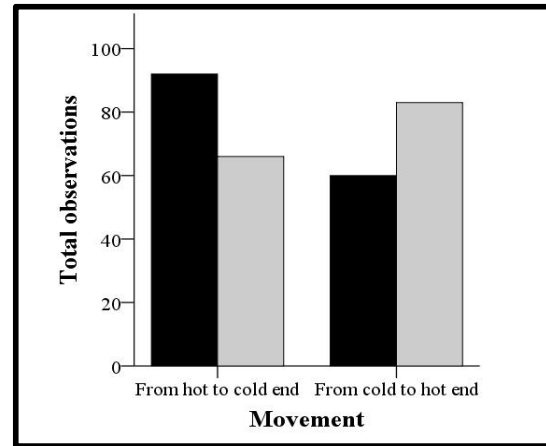


FIGURE 4. Movements of Tuatara (*Sphenodon punctatus*) from area 4 to area 1 (hot to cold: -3 movements) and from area 1 to area 4 (cold to hot: +3 movements) during the day (grey bars 0800–1700) and night (black bars 1800–0700).

0.970), and none of the interactions were significant. An analysis on the subset of data in which Tuatara moved the length of the gradient within one hour revealed that time was the only predictor of movement from one extreme to the other (Wald $\chi^2 = 8.335$, $df = 1$, $P = 0.004$), with more movements of Tuatara from hot to cold during the night and more from cold to hot during the day (Fig. 4).

DISCUSSION

Temperature is important for reptiles but the ecological performance of the animal depends on many factors in its environment, not just its thermal physiology (Huey 1991). Environmental constraints will limit thermoregulatory precision of any animal, despite thermoregulatory effort. For Tuatara, such constraints include low ambient temperatures, possible high densities, conspecific competition for burrows, and the annual presence of seabirds during their breeding season, all of which may lead to competition for the most suitable burrows. The present study suggests that Tuatara seek out and remain longer at warmer burrows, and are more active under humid conditions.

Temperatures selected.—The temperatures selected by the juvenile Tuatara in this study were consistent with previous gradient studies (mean range: 17–21° C, Stebbins 1958; mean range: 19–25° C, Besson and Cree 2010b), and reveal that Tuatara exhibit a preference for temperatures around 20° C, regardless of digestive state, humidity, or time of day. In contrast to previous studies (Besson and Cree 2010a), this study revealed a clear diel trend in thermoregulatory behavior. The mean temperature selected during the day was 1.0° C higher than that selected at night, as more Tuatara chose to position themselves in the warmest quarter of the gradient during the day than at

night. Both diurnal and nocturnal reptiles often select cooler temperatures at night than during the day (Rismiller and Heldmaier 1982; Innocenti et al. 1993; Refinetti and Susalka 1997; Ellis et al. 2006), and in the wild, Tuatara would naturally be exposed to colder temperatures at night. As a compensatory mechanism, nocturnal lizards may have higher performance capacity at low temperatures than do comparable diurnal lizards (Autumn et al. 1994). Unlike most other reptiles, Tuatara are active at temperatures as low as 5.2° C and thus are well adapted to emerge at night under cold conditions (Thompson and Daugherty 1998). During the day, Tuatara bask in areas of sun and can obtain temperatures of up to 34.5° C (Ilse Corkery, unpub. data). Basking behavior that raises body temperature may be important in maximizing foraging ability, as high daytime temperatures are followed by an increase in nocturnal Tuatara activity (Walls 1983). However despite a temperature band of 26–30.5° C in area 4, and a high percentage of Tuatara using area 4, the average daytime temperature was significantly lower. One explanation could be that tuatara moved between areas more than the hourly recording captured or spent more time on top of burrows where the air temperature was cooler.

A reduction of preferred temperature under arid conditions could be viewed as an adaptation to facilitate survival on land (Malvin and Wood 1991). As such, a response would lower the driving gradient for evaporative water loss, thereby conserving water. However, in this study, juvenile Tuatara tended to select higher body temperatures and we found them most often in the warmest quarter of the gradient under the dry treatment. There are few previous studies investigating the relationship between humidity levels of the atmosphere and/or dehydration and body temperatures in ectotherms, and those that do report conflicting findings. The anneliid lizard, *Anniella pulchra*, selected lower temperatures in a dry thermal

gradient than in a moist one (Bury and Balgooyen 1976), but in the Desert Iguana (*Dipsosaurus dorsalis*), there was no effect of dehydration to 80% initial body weight on behavioral thermoregulation on a thermal gradient (Dupré and Crawford 1985). One explanation for our findings is that any additional water loss due to evaporative cooling during the dry treatment was negated by the fact that Tuatara had access at all times to fresh drinking water. It may also be that in a longer experiment, humidity has a greater influence on behavior. Further studies to investigate the extent to which thermoregulation may be limited by the hydric environment of the Tuatara would be useful.

Although statistically significant, the mean body temperature differences between both day and night and between humidity treatments were only 1° C. This difference may not be biologically significant, and would likely be increased in natural conditions where higher variability in temperature would occur between day and night. It is unknown whether a one degree difference in mean body temperature could affect Tuatara, as the thermal sensitivity of physiological processes (apart from metabolic rate: Wilson and Lee 1970; Cartland and Grimmond 1994) in Tuatara has received little attention. The mass-specific resting metabolic rates of juvenile Tuatara increase over an ambient temperature range of 5.0–22.5° C (Cartland and Grimmond 1994) as expected, as the metabolism of ectotherms is strongly temperature-dependent (Bennett 1988). However, despite relatively low differences in body temperature, the behavioral data from this study suggest that Tuatara are selecting areas based on temperature, with a difference of ~10% in the number of animals recorded in the warmest end of the gradient between day and night, and between dry and humid treatments.

Digestive state had no discernable effect on either temperatures selected or burrow use. Support for the idea that animals select body temperatures depending on fed versus fasted state to facilitate a trade-off between energy balance and digestive efficiency is not always evident in the field either (Brown and Griffin 2005). However, it is possible that the absence of predators and the continual availability of a wide range of temperatures in the present study resulted in juvenile Tuatara that were not subjected to the same pressures regarding digestion as they would face in the field. In addition, it may also be that digestive state is not the deciding factor in terms of thermoregulation or that temperature is a greater limiting factor so that Tuatara seek warmer temperatures regardless of digestive state.

Burrow use and movement on the gradient.—We found twice as many Tuatara outside their burrows during the night compared to during the day, and significantly more activity (movement on the gradient) during the night. Nocturnal geckos are typically active at body temperatures that are far below their preferred

body temperatures (Angilletta and Werner 1998; Hare et al. 2007), which Autumn et al. (1994) demonstrated can reduce the energy expended on maintenance and activity. Nocturnal insects make up a large proportion of the Tuatara's diet (Walls 1981), however; in addition, Tuatara may also be more active at night to reduce energetic costs associated with warmer temperatures. This is an additional area that warrants further research.

Under the humid treatment, we recorded significantly more Tuatara outside their burrows in comparison to the dry treatment. Humidity has only rarely been monitored during investigations of reptile behavior, but one such study revealed that the activity patterns of the Malayan Pit Viper (*Calloselasma rhodostoma*) were found to be more strongly correlated with variation in relative humidity than with temperature, with more snakes active on humid nights (Daltry et al. 1998). Anecdotal evidence also suggests that Tuatara are more active and are out in greater numbers on damp, misty nights (Newman 1977; Barwick 1982).

Implications of this research.—Both Tuatara body temperature and burrow use are influenced by humidity levels. In temperate environments, with temperature often a limiting factor for thermoregulation, humidity may be a lesser factor governing the activity patterns of reptiles. However, for some species such as the Tuatara, which are often restricted to islands on which there are no standing bodies of freshwater, humidity may indeed play a greater role in determining habitat selection and timing of activity. Water loss may be the over-riding factor that reduces nocturnal and daytime activity during warm or dry periods, or indeed the factor that governs the number of days that an animal can repeatedly bask (Barwick 1982). Thus, any advantage in terms of water conservation could potentially enhance fitness. Higher humidity could facilitate extended activity periods and perhaps enable extended feeding into winter. The lowest humidity recorded on Stephens Island over the period of one year (2008) was 48% RH (Stephens Island weather station; extracted from National Institute of Water and Atmospheric Research. 2011. National climate database. Available from <http://cliflo.niwa.co.nz/> [Accessed April 2011]), which is within the humidity range of the “dry” treatment of this study, but humidities of 100% were regularly recorded on Stephens Island. It is therefore possible that the “humid” treatment needed to be set closer to 100% humidity to draw out any behavioral differences.

The features of habitats that make them suitable for a particular species are of considerable significance for understanding phenomena such as the distribution, abundance, and conservation status of that taxon (Shah et al. 2004). This study provides experimental evidence that reptiles are capable of adjusting their microhabitat selection behavior in response to

different humidity constraints. Temperature selection may change based on humidity, but perhaps more importantly, burrow use and activity changes with humidity. This may have important implications for the conservation of Tuatara, particularly in the light of on-going climate change. If Tuatara limit their activity to humid periods, they may be forced to remain in burrows during dry spells. This could ultimately have negative impacts on their ability to forage, grow, and reproduce.

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