

# An assessment of thermal preference of two species of Knob-tailed Geckos, *Nephrurus levis* and *N. laevis*, at Uluru Kata-Tjuta National Park

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## Abstract

Nocturnal lizards are often active at temperatures that are sub-optimal for physiological functioning, a phenomenon that has been referred to as the ‘nocturnal paradox’. The purpose of this study was to investigate the general habitat and thermal preference of two species of nocturnal gecko in the genus *Nephrurus* with a focus on differences between preferred body temperatures determined under laboratory conditions and those measured in animals at the time of field collection. The Smooth Knob-tailed gecko (*Nephrurus levis*) and the Pale Knob-tailed Gecko (*N. laevis*) inhabit the desert environment of Uluru Kata-Tjuta National Park in the Northern Territory of Australia. Habitat preferences were determined by documenting capture locations for these species while thermal preferences were determined using laboratory-based thermal gradients. Analysis of habitat use demonstrated a significant difference in habitat preference between the two species. *Nephrurus levis* was most often in *Spinifex* sandplain and mulga shrubland and *N. laevis* was most often found around sand dune habitats. Field-active body temperatures of both species ranged from 14.5 °C to 32.2 °C and were significantly correlated with air and ground temperature at the time of capture. The thermal preference ( $T_{pref}$ ) of *N. levis* (mean day  $T_{pref_{mid}} = 29.1$  °C and mean night  $T_{pref_{24}} = 28.2$  °C,  $n = 19$ ) and *N. laevis* (mean day  $T_{pref_{mid}} = 29.5$  °C and mean night  $T_{pref_{24}} = 27.8$  °C,  $n = 27$ ) were not significantly different, although both species exhibited significantly higher daytime and night-time preferred body temperatures than body temperatures observed in the field. Body size did not affect thermal preference for either species. As such, the thermal preferences of these species support the concept of the nocturnal paradox. Additionally, it has been suggested that the characteristic swollen tail tip displayed by all *Nephrurus* species may play a role in assessing the thermal environment. While not investigated extensively here, combined data for both species demonstrated that individuals oriented their tail toward the heat source in thermal gradients significantly more than expected if orientation were random.

## Introduction

Nocturnality in reptiles has been called a paradox since the organisms are commonly active at temperatures that are sub-optimal for traits such as sustained locomotion, sprint speed, growth and possibly auditory sensitivity (Campbell 1969; Huey *et al.* 1989; Autumn & DeNardo 1995; Autumn *et al.* 1999). For example, preferred body temperatures ( $T_{pref}$ ) in nocturnal geckos, determined by measuring the body temperatures selected by lizards in a laboratory thermal gradient, have been found to range between 25 °C to 35 °C (Dawson 1975; Angilletta & Werner 1998; Huey *et al.* 1989; Angilletta *et al.* 1999), which is higher than active nocturnal foraging body temperatures that have been recorded as low as 15 °C in some species (Meiri *et al.* 2013). Nocturnality in lizards may therefore represent a trade-off between physiological performance and access to an unexploited niche (Vitt *et al.* 2003). In the specific case of geckos, termites may have been a driver for the evolution of nocturnality since termites and their invertebrate predators are often active above ground at night (Morton & James 1988). Additionally, as termites occur in colonies, such a concentrated food supply assures that the profits gained from this resource will generally outweigh the costs of finding it (MacArthur & Pianka 1966; Pianka & Pianka 1976). Activity at night may also facilitate predator avoidance, as many lizard predators (e.g. birds) are either inactive at night or have decreased capacity to see prey. Additionally, studies have shown that nocturnal lizards have a lower cost of locomotion than their diurnal counterparts (Autumn *et al.* 1994, 1997, 1999), which may impart additional advantages.

One genus of gecko that has received limited attention in thermal studies is *Nephrurus*, the knob-tailed gecko. Pianka & Pianka (1976) reported that the field active body temperature ( $T_b$ ) of 12 nocturnal lizard species in Western Australia, including the Smooth Knob-tailed Gecko (*N. levis*), the Pale Knob-tailed Gecko (*Nephrurus laevis*), and the Midline knob-tailed Gecko (*N. vertebralis*), were strongly correlated with ambient air temperatures ( $T_a$ ). These data suggest that these species may be predominately thermoconforming to environmental temperatures during activity. The only published  $T_{pref}$  data for *Nephrurus* is by Angilletta & Werner (1998), who recorded a mean  $T_{pref}$  of 25.1 °C for the Starred Knob-tailed Gecko (*N. stellatus*). Such a gap in  $T_{pref}$  data for *Nephrurus* geckos hinders the interpretation of  $T_b$  data. Additionally, a notable and unique feature of this genus is the swollen knob at the tip of the tail. The function of the caudal knob is still largely unknown, however some have suggested it may play a role in assessing the thermal environment (Russell & Bauer 1987).

Two species of *Nephrurus*, *N. levis* (Figure 1) and *N. laevis* (Figure 2), inhabit the central Australian deserts, where they are relatively abundant and can be found foraging at night on the open sand of dunes and sandplains. Although these two species are similar in morphology, they have been reported occupying different microhabitats within the Australian landscape. Studies have found that *N. levis* appears to prefer sandplain habitats, at least in the western half of its range, whilst *N. laevis* generally occupies sand dune habitats (Pianka 1969; Pianka 1972; Pianka & Pianka 1976). The



**Figure 1.** Smooth Knob-tailed Gecko (*Nephrurus levis*). Uluru Kata-Tjuta National Park. Captive individual in thermal gradient. (Brenton Hays)



**Figure 2.** Pale Knob-tailed Gecko (*Nephrurus laevis*). Uluru Kata-Tjuta National Park. Captive individual in thermal gradient. (Brenton Hays)

environment and ecology of the two species offers an ideal framework for an investigation of how temperatures selected in a thermal gradient, i.e. thermal preference ( $T_{pref}$ ) compare to field-active body temperatures ( $T_b$ ) experienced at night. This study had two aims; 1) to measure temperature selection ( $T_{pref}$ ) for *N. levis* and *N. laevis* in a laboratory thermal gradient and 2) to compare  $T_{pref}$  with  $T_b$  both within and between the two species. As a secondary objective, this study aimed to collect preliminary data regarding the role of the tail knob in the animal's assessment of the thermal environment.

## Materials and Methods

### *Study site*

Geckos were sampled from Uluru Kata-Tjuta National Park between September and November 2013 during peak activity times for the study species. The Park covers an area of 1325 km<sup>2</sup> and contains two major rock formations: Uluru

and Kata-Tjuta. The climate in the area is arid, with low rainfall (generally occurring in summer) and high evaporation (Reid *et al.* 1993). Mean daily minimum and maximum air temperatures range from 20.9 °C to 37.5 °C in January (mid-summer) and 3.4 °C to 20.3 °C in July (mid-winter) (Australian Government Bureau of Meteorology 2014).

### *Field collection*

Surveys typically commenced at approx. 20.00 hr and continued for an average of four hours. Survey sites were chosen based on known *Nephrurus* habitat (Pianka & Pianka 1976; Reid *et al.* 1993), including sand dunes (crest and swale), *Spinifex* sandplains, and Mulga shrublands. Using a head torch and hand-held flashlight, geckos were detected by movement or eye shine. At times geckos were also sampled via vehicle cruising on the bitumen roads and dirt tracks. Once detected, geckos were captured by hand

as quickly as possible. Once captured, body temperature was measured within 15 sec of handling (Mayhew 1963) by inserting the thermocouple of a Fluke® 566 infrared thermometer (Fluke Australia Pty Ltd, Castle Hill, NSW) in the cloaca. This temperature was recorded as the gecko's field-active body temperature ( $T_b$ ). Air ( $T_a$ ) and ground ( $T_g$ ) temperature were also recorded at the site of capture. Air temperature was measured by placing the Fluke® thermocouple approximately 5 cm above the ground surface. The infrared thermometer was also used to measure ground surface temperature. Habitat type where geckos were sampled was noted as sand dune, *Spinifex* sandplain, or mulga shrubland. For the purpose of this study, sand dune habitats included the swale, which was classified as the area surrounding the dune to a distance of approximately 25 m, depending on both the distance to neighbouring dunes and the slope of the ground (i.e. the base of some dunes were more obvious than others). Identification of habitat types followed descriptions by Pianka (1972), Buckley (1981) and Saxon (1984). Geckos were then placed in marked cloth bags and stored temporarily in an ice-chilled (approx. 10 °C) and insulated cooler for transportation back to the laboratory (Klawinski *et al.* 1994). Sites where geckos were found were not revisited to reduce the likelihood of double sampling.

#### *Measurement of thermal preference*

The laboratory in which the thermal preference experiments were conducted was a 10 x 3 m demountable building located within the national park. Thermal preference was measured using thigmothermic thermal gradients based on design specifications used by Angilletta & Werner (1998). Thermal gradients were constructed from 12 mm plywood for the sides and 2 mm galvanised steel for the base. Fine sand sampled from the top of a sand dune was spread approximately 5 mm across the metal base to provide substrate. Each gradient was 1200 x 600 x 200 mm and consisted of three separate runs. Three of these gradients were constructed, accommodating nine geckos at any one time. A temperature gradient was created using 120-watt heat lamps for the heat source (one heat lamp per run) and six ice bricks (two stacked on top of one another beneath the metal base for each run) to cool the other end. Ice-bricks were small (165 x 950 x 20 mm) hard plastic water receptacles that could be frozen (typically used to keep food cold).

To achieve a suitable thermal environment, thermal gradients were tested and calibrated over a period of a week prior to the commencement of experiments. This involved recording temperature in the gradients by placing individual iButton® temperature data loggers (Maxim Integrated, San Jose, California) spaced 24 cm apart down the length of the run for a period of 24 hr. Tests were run in each of the different gradients to ensure no differences between them. To delay melting, the ice bricks were insulated on the bottom and sides with polystyrene, leaving the top open to be in direct contact with the metal base of the thermal gradients. By changing the ice bricks every 8 hr, the cool end of the gradient was kept stable. Tests with iButton® data loggers demonstrated a temperature gradient ranging from 17–62 °C was achieved. The lighting regime in the

laboratory followed a day/night light cycle that was very similar to what these nocturnal geckos would experience in the field (i.e. dark most of the time). The windows of the demountable building were blocked with curtains to reduce incident sunlight. At night, room lighting was limited to short periods only when required. An iButton® was also placed outside the gradient during tests to confirm room temperature remained within one degree of 20 °C.

Thermal preference experiments were typically commenced within 1 hr of returning the geckos to the laboratory after capture. Each gecko was placed in the centre of the thermal gradient and its entry time noted. Thermal preference experiments were conducted for 24 hr, during which two temperature measurements were taken: one at midday to represent day-time preference ( $T_{pref_{mid}}$ ) and another after 24 hr for night-time preference ( $T_{pref_{24}}$ ). These temperatures were classified as 'preferred' body temperatures ( $T_{pref}$ ).  $T_{pref_{mid}}$  was measured between 12.00 hr and 13.00 hr using the Fluke® infrared thermometer (distance to spot ratio of 30:1) pointed at the gecko's lower back and base of tail, close to the cloaca at a distance of approximately 5 cm to give an infrared spot size of approximately 2 mm. Infrared measurements were taken at this mid-point of the experiment (versus determining the cloacal temperature) to minimise disturbance to the geckos.  $T_{pref_{24}}$  was measured by inserting the thermocouple of a Fluke® 566 infrared thermometer (Fluke Australia Pty Ltd, Castle Hill, NSW) in the cloaca after each gecko had been in the thermal gradient for 24 hr. Additionally, at the time of  $T_{pref_{24}}$  measurement, the orientation of each gecko's tail was noted with respect to the heat source. Gecko tails classified as pointing 'toward' were closer to the heat source than the head. Accordingly, tails classified as 'away' were further than the head from the heat source.

Body measurements were taken at the conclusion of thermal preference experiments. Snout-vent length was measured to the nearest 1 mm using a clear plastic ruler. Body mass was measured to the nearest 0.1 gm using Pesola® spring scales (Pesola AG, Baar, Switzerland). Additionally, whether the tail was original or regrown was noted. Regrown tails are easily identified by the absence of the characteristic caudal knob (Russell & Bauer 1987). After measurements were completed, the geckos were again placed in individual cloth bags and stored in an ice-chilled cool box. Each gecko was then transported to, and released within, a few metres of the original flagged capture location.

### *Analysis*

Comparison of gecko distributions between habitats and gecko tail orientations after 24 hr in the thermal gradients were conducted using a Chi-square Goodness of fit Test at  $\alpha = 0.05$  in SigmaPlot Version 11 (Systat Software, Inc., San Jose, California). Relationships between field body temperatures and mass and field body temperatures and air and ground temperatures were assessed using linear regression in SigmaPlot Version 11 as well. Both temperature and mass data for the two species were combined for these analyses. All other statistical tests were conducted using the PROC GLM procedure

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in SAS 9.4 (SAS Institute, Inc., Cary, North Carolina), with all comparisons made at  $\alpha = 0.05$ . Because of the imbalance in sample sizes (numbers of animals collected per species, by sampling date, or in different habitats), we used the Type III Sum of Squares in determining significance in the Analysis of Variance (ANOVA) tests used. Gecko morphometric parameters were compared using a one-factor ANOVA with species as the main effect followed by the Tukey method for post-hoc comparisons. Ground and air temperatures were similarly compared using a two-factor ANOVA with month and habitat as the main effects. Gecko field body temperatures between species were compared using an Analysis of Covariance with mass as the covariate, and differences between field body temperatures and preferred body temperatures at midday and 24 h ( $T_{pref_{mid}}$  and  $T_{pref_{24}}$ ) were determined using a repeated measures ANOVA.

## Results

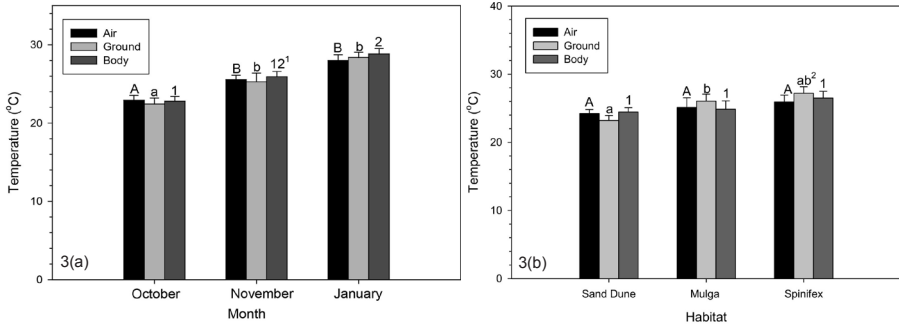
### *General habitat use and body size of the test species*

A total of 27 *N. levis* and 52 *N. laevis* were captured within Uluru Kata-Tjuta National Park during the surveys reported here. The geckos demonstrated a significant difference in habitat use ( $\chi^2 = 53.3$ ,  $p < 0.001$ ), with *N. levis* primarily found in *Spinifex* sandplains (63%), mulga shrublands (30%), and occasionally on sand dunes (7%). In contrast, *N. laevis* was mostly found around sand dunes (90%), and occasionally in *Spinifex* sandplains (10%) in areas of open sand within short distances of a *Spinifex* tussock.

The average mass and SVL for *N. levis* (17.2 gm and 86.3 mm, respectively) were both significantly greater ( $p < 0.0001$ ) than those for *N. laevis* (7.3 gm and 67.6 mm, respectively, Table 1. A linear regression of field body temperature versus mass for all animals collected indicated a significant relationship ( $p = 0.019$ , Body temperature =  $22.8 + (0.198 * \text{Mass})$ ), although the  $r^2$  value of 0.08 indicates mass did not explain much of the variation in body temperature. The average field body temperature for *N. levis* measured for the animals over the course of the study (26.2 °C) was also higher than that for *N. laevis* (24.5 °C) but this difference was not significant based on an ANCOVA with mass as the covariate. It is interesting to note that while the maximum field body temperature measurements were similar between the species, *N. laevis* had a lower minimum recorded temperature which could account for the lower overall average body temperature for the species.

**Table 1.** Average morphometric and field body temperatures across all sampling dates for *Nephrurus levis* and *N. laevis*. Numbers in parentheses are 1 standard error of the mean and the range of values recorded.

	<i>Nephrurus levis</i>	<i>Nephrurus laevis</i>
Mass (g)	17.2 (1.1, 9.0–25.6)	7.3 (0.5, 1.5–15.0)* $p < 0.0001$
SVL (mm)	86.3 (2.4, 62.0–112.0)	67.6 (1.7, 41.0–86.0)* $p < 0.0001$
Field body temp (°C)	26.0 (0.8, 19.5–33.5)	24.5 (0.6, 14.5–33.6)



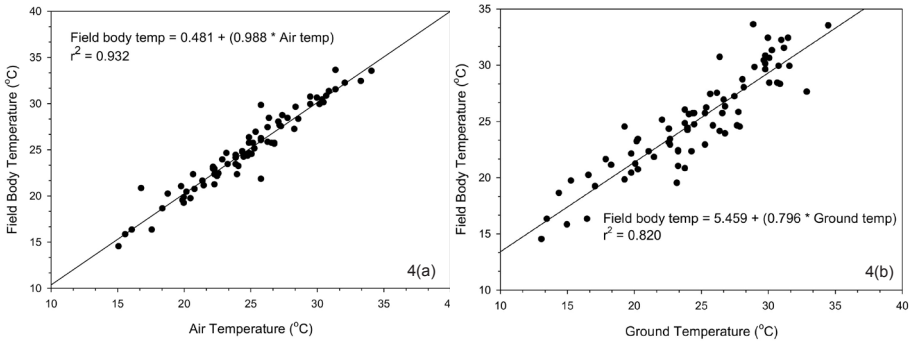
**Figure 3.** Average air, ground and gecko body temperatures based on sampling month (a) and habitat (b). For air temperature, bars that do not share a common upper-case letter are significantly different at  $\alpha=0.05$ , for ground temperature significant differences are indicated by bars that do not share a lower case letter, and for body temperature significant differences are indicated by bars that do not share a common number. Error bars represent 1 standard error of the mean. <sup>1</sup>p-value for November vs. January body temperatures = 0.0576, <sup>2</sup>p-value for Sand vs. *Spinifex* ground temperature = 0.0519.

We also compared air temperature, ground temperature, and combined field body temperatures within and across the sampling months of October, November, and January (Figure 3a), and within and between habitats (Figure 3b). There were no significant interactions between any combination of sampling month or habitat for any temperature variables. There was also no significant effect of species on field body temperature. Air and ground temperatures were significantly cooler in October as compared to November and January (Air temp: October vs November,  $p=0.033$ ; October versus January,  $p<0.0001$ ; Ground temp: October versus November,  $p=0.027$ ; October versus January  $p<0.0001$ ). Average field body temperature was significantly lower in October than in January (22.8 versus 28.8,  $p<0.0001$ ). Field body temperature was also lower in November as compared to January, but this was just on the limit of statistical significance (25.9 versus 28.8,  $p=0.0576$ ). There were no significant differences in air or body temperatures between the three habitat types, but ground temperature in the sand dune habitat was significantly lower than that in Mulga (23.2 versus 26.0,  $p=0.0324$ ) and nearly significantly lower than that in *Spinifex* (23.2 versus 26.5,  $p=0.0519$ ).

To further evaluate the degree of thermoconformity the geckos exhibited to environmental temperatures, the combined field body temperature data for both species were regressed against air (Figure 4a) and ground temperatures (Figure 4b). Significant positive relationships were detected between body temperature and both air ( $r^2 = 0.932$ ,  $p < 0.001$ ) and ground temperature ( $r^2 = 0.820$ ,  $p < 0.001$ ), with field body temperature displaying a slightly stronger relationship with air temperature.

### *Thermal preferences*

For both *N. levis* and *N. laevis*, the average  $T_{pref_{mid}}$  of 29.1 °C (range: 24.6–38.7 °C), and 29.4 °C (range: 20.9–34.6 °C, respectively), was significantly greater than the average  $T_b$  (Figure 5). Similarly, the average  $T_{pref_{24}}$  of 28.1 °C (range: 24.5–32.5 °C) and 27.8 °C

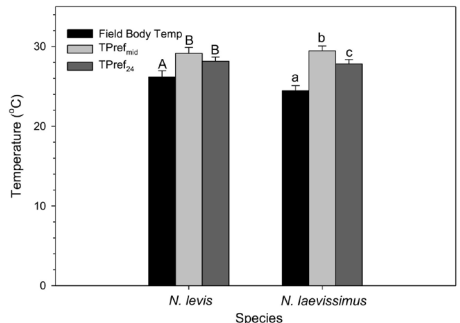


**Figure 4.** Relationship between field-active body temperature and air (a) or ground (b) temperature at place of capture across all habitats for both *Nephus levis* and *N. laevis*.

(range: 20.9–34.6 °C), respectively, were also significantly greater than their  $T_b$  ( $P < 0.0001$  for all comparisons except  $T_{pref_{24}}$  vs. field body temp for *N. levis*, for which  $p = 0.0002$ ). No significant differences were detected in the  $T_{pref}$  measurements between each species.

*Tail orientation and autotomy*

To examine the potential role of the tail in assessing the thermal environment, tail orientation at the time the  $T_{pref}$  measurements were taken was recorded. Orientation of the tail was classified as either pointing ‘away’ or ‘toward’ the heat source, with the expected frequency based on an equal number of individuals between the two orientations. No significant difference was detected between observed and expected tail orientations for either *N. levis* or *N. laevis*. However, for both species, approximately 67% of individuals orientated their tails ‘toward’ the heat source (Table 2). Analysis of data for both species combined demonstrated a significant difference between the observed frequency of individuals orienting their tail toward the heat source and the expected frequency ( $\chi^2(1) = 5.56, p < 0.05^*$ ).



**Figure 5.** Average field and preferred body temperatures at midday and 24 h for *Nephus levis* and *N. laevis*. For *N. levis*, bars that do not share a common upper-case letter are significantly different at  $\alpha = 0.05$ . For *N. laevis* significant differences are indicated by bars that do not share a lower-case letter. Error bars represent 1 standard error of the mean.

Evidence of autotomy (i.e. absence of caudal knob) was apparent in 28% of *N. levis* captured. The selection of  $T_{pref}$  by *N. levis* with regrown tails was not significantly different to geckos with original tails. This comparison could not be conducted for *N. laevis* because no captured individuals of this species displayed evidence of tail autotomy.



**Table 2.** Observed tail orientation after 24 h in the thermal gradient for both *Nephrurus levis* and *N. laevisissimus* individually and combined. Orientation of tail was classified as either pointing ‘away’ or ‘toward’ the heat source. Critical values from Chi-Square Goodness of Fit test and associated P-values are based on expected equivalent distributions of individuals in the two orientation categories.

	<i>Nephrurus levis</i>		<i>Nephrurus laevisissimus</i>		<i>Combined</i>	
	Toward	Away	Toward	Away	Toward	Away
Observed	13	6	18	9	31	15
Expected	8.5	8.5	13.5	13.5	23	23
Critical, p-value	3.11, 0.077		3.00, 0.083		5.57, 0.018*	

\* Statistically significant at  $\alpha = 0.05$ .

## Discussion

### *Field body temperatures and thermal preferences*

Statistically significant relationships between field-active body temperature ( $T_b$ ) and environmental temperatures measured at the capture location ( $T_a$  and  $T_g$ ) in this study suggest that these two *Nephrurus* species may not be behaviourally thermoregulating at night. The strong relationships meet Huey & Slatkin’s (1976) criteria for thermoconformity and suggest that both *N. levis* and *N. laevisissimus* may be mostly thermoconforming at the prevailing environmental temperatures for this study. This is consistent with previous studies describing thermoconformity during activity by *Nephrurus* congeners (Licht *et al.* 1966; Pianka & Pianka 1976) and other nocturnal ectotherms including other gecko species, lizards (e.g. *Zootoca*) and iguanas (e.g. *Sphenodon*) (Huey 1974; Herczeg *et al.* 2003; Wu *et al.* 2009; Tan & Schwanz 2015). One limitation to this conclusion, however, is that this study did not measure the range of available microhabitat temperatures at each capture location, which is necessary for a truly comprehensive description of temperature regulation (Hertz *et al.* 1993). Thermoregulation at night has previously been reported for nocturnal thigmotherms (Rock & Cree 2008; Tan & Schwanz 2015), although the high energetic cost of behavioural thermoregulation is suggested to be a factor influencing its use (Huey 1974).

$T_{pref}$  selected by *Nephrurus* geckos in the thermal gradients were similar to those reported for other gecko species (Angilletta and Werner 1998; Angilletta *et al.* 1999; Kearney & Predavec 2000; Hitchcock & McBrayer 2006; Tan & Schwanz 2015), although  $T_{pref}$  for both species were higher than both the day (24.2 °C) and night (26 °C)  $T_{pref}$  reported for *N. stellatus* (Angilletta & Werner 1998). One potential problem with our  $T_{pref}$  estimates is that they are based on single measurements of the geckos taken at midday and midnight. As such, we may be presenting a body temperature of the animal in some phase of behavioural thermoregulation rather than a truly “preferred” temperature. Other studies that have investigated thermal preferences in geckos have relied on multiple measurements of body or substrate temperature taken over the course of the time they are in the thermal gradients (e.g. Angilletta & Werner 1998; Angilletta *et al.* 1999; Tan &

Schwanz 2015). While the movement patterns of geckos in this study were not closely monitored, the majority of individuals were often found partially buried in the thin layer of sand of the thermal gradient when the temperature measurements were taken, indicating they had been in place for at least some period of time. Additionally, the variability in the  $T_{pref}$  temperatures reported here are comparable to that reported in the previously cited studies that used continuous monitoring (e.g.  $1 SE < 1$ ) and the temperature ranges are also comparable to those studies in which range was reported. We therefore feel our reported temperatures are reasonable approximations of a preferred body temperature for the geckos.

While *N. levis* and *N. aevissimus* did not significantly differ in  $T_{pref}$ , *N. levis* displayed a significantly higher mean  $T_b$  (24.7 °C) than *N. laevisissimus* (22.3 °C). This difference may be driven by substrate differences between the habitat types. Although we found no difference in air temperature between habitats, the average ground temperature in sand dunes was significantly lower than in Mulga and nearly significantly lower than that for *Spinifex* sandplain habitats. Sand dunes have soft, sandy soil, which is known to be more thermally diffusive than the clayey sands and soils of sandplains and shrublands (De Silans *et al.* 1996), therefore leading to more rapid loss of heat. The lower minimum  $T_b$  recorded for *N. laevisissimus* may reflect the lower substrate temperatures in the sand dunes where this species was common and in turn the lower average  $T_b$ .  $T_b$  measurements for *N. levis* and *N. laevisissimus* were lower and more variable than both  $T_{pref_{mid}}$  and  $T_{pref_{24}}$ , which is consistent with the idea of the nocturnal paradox. These results are also consistent with previous studies comparing  $T_b$  and  $T_{pref}$  (Huey & Bennett 1987; Angilletta & Werner 1998; Gil *et al.* 1994; Angilletta *et al.* 1999; Hitchcock and McBrayer 2006; Wu *et al.* 2009; Tan & Schwanz 2015).

However, the paradox discussion is generally based around body temperatures that are optimal for locomotion, as that is considered to be one of the most important physiological functions during activity (Autumn *et al.* 2002). Our study measured the body temperatures selected by *Nephrurus* geckos in a thermal gradient and it is unknown how these may compare to body temperatures optimal for sprint performance. In diurnal lizards, these two temperatures have been reported as being very similar (Huey & Bennet 1987; Angilletta *et al.* 2002; Lailvaux *et al.* 2003). Although the nocturnal and diurnal lizards studied by Huey & Bennet (1987) exhibited a similar optimal sprint performance body temperature, their nocturnal subject species, including Royal Ctenotus (*Ctenotus regius*), Copper-tailed Skink (*C. taeniolatus*) and Spotted Ctenotus (*C. uber*), actively selected a much lower  $T_{pref}$  in the thermal gradient. This suggests that the selection of  $T_{pref}$  in lizards may not always prioritise locomotion.

Most nocturnal ectotherms thermoconform to environmental temperatures during activity due to limited thermal variation (Pianka & Pianka 1976; Licht *et al.* 1966; Herczeg *et al.* 2003; Hitchcock & McBrayer 2006; Wu *et al.* 2009; Tan and Schwanz 2015). Therefore, behavioural thermoregulation may be largely confined to daytime refuge sites as the soil offers a vertical thermal profile (Körtner *et al.* 2008). It is possible

that selection of body temperatures during refuge would more likely reflect priorities of metabolism, digestion and growth than sprint speed (Kearney & Predavec 2000). This notion is supported by Carretero *et al.* (2005) who suggest that temperature preference should be interpreted as a compromise between selective pressures, both from the thermal environment and energy allocations/requirements. To better understand the physiological significance of these  $T_{pref}$  exhibited by *N. levis* and *N. laevis*, further work is required involving testing optimal temperatures for various physiological and behavioural functions and evaluating these based on measured temperatures in daytime burrows.

### *Tail orientation and autotomy*

The only extensive investigation of the *Nephrurus* tail knob, including histological and anatomical characterisations, was conducted by Russell & Bauer (1987). They concluded it had a probable functional role in monitoring the thermal environment. However, to date there has been no other strong evidence to explain the function of the unique tail morphology. Analysis of tail orientation by *N. levis* and *N. laevis* geckos in the thermal gradient suggests that *Nephrurus* geckos are selectively positioning their caudal knob towards the heat source similar to the direction they are reported to be orientated within their burrow during the day (Pianka & Pianka 1976). These results may provide evidence to support the idea that the tail plays some role in assessing the thermal environment, although just what that role might be is unclear.

Autotomy frequencies in *Nephrurus* are low by gecko standards. Russell & Bauer (1987) and Pianka & Pianka (1976) found that *N. laevis* had the lowest (0.6%) reported frequency of the 12 nocturnal lizards they investigated in the Western Australian desert. The present study supports these observations, with none of the 52 *N. laevis* captured exhibiting signs of autotomy and only a limited number of *N. levis* exhibiting it. The frequency of tail autotomy is said to be driven by both the number of autotomy sites in the tail and the cost of tail loss to the individual (Bateman & Fleming 2009). *Nephrurus* exhibits only a basal autotomy site which may indicate the cost of losing the tail outweighs the benefit of its loss. This may support the idea that the tail knob plays some important physiological role. Regrown tails are reported to show skeletal, neural, and muscular differences as compared to original tails (Bellairs & Bryant 1985), which could influence sensory capacity of the structure if such a role exists. However, we found no significant difference in  $T_{pref}$  between *N. levis* with original and regrown tails.

### *Summary*

The results of this study indicate that *N. levis* and *N. laevis* exhibit size and habitat use differences that may lead to a slight difference in field body temperature. However, we demonstrate that both species are predominantly thermoconforming during activity and often do not reach their  $T_{pref}$ , that is, they exhibit the ‘nocturnal paradox’. This study adds recent and relevant data to a relatively dated body of literature on thermal preference in nocturnal reptiles. Further investigation of the thermal environment of

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the daytime burrow for these species and the associated body temperatures therein provide an interesting area for further research. Individuals from both species also had a greater propensity to orient the tail knob toward the heat source in the thermal gradient experiments, although no temperature differences were observed between geckos that had lost and regrown tails and those that had not. The frequency of tail autotomy was low in field-collected animals and the role this structure may play in the thermal biology of these organisms remains unclear.

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