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Heat seekers: A tropical nocturnal lizard uses behavioral thermoregulation to exploit rare microclimates at night

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ABSTRACT

Environmental temperatures play a vital role in the physiological and behavioral activity of ectotherms. Behavioral thermoregulation allows animals to modify their body temperature to optimize functions critical to fitness, including digestion, growth, reproduction, and locomotor performance. Diurnal reptiles are a classic model system to answer questions related to thermal ecology, whereas behavioral thermoregulation in nocturnal species is thought to be strongly constrained by low environmental thermal heterogeneity at night. The few studies describing the thermal ecology of nocturnal reptiles indicate a majority of thermoregulatory behavior (if any) occurs during the day within diurnal retreats, but few examined this behavior throughout the night. In tropical systems, thermal heterogeneity may remain high, even at night, allowing nocturnal ectotherms to thermoregulate through conduction on surfaces that retain heat after sunset. We investigated the thermoregulatory behavior of a tropical nocturnal gecko (Australian house gecko, *Gehyra dubia*) by measuring its preferred temperature in a thermal gradient, and selected body temperatures using radio telemetry, in relation to available operative environmental temperatures obtained using thermal models. Preferred body temperatures of geckos ranged from 31.4 ± 0.59–34.5 ± 0.55 °C in a laboratory thermal gradient. In the field, during winter, geckos were more effective thermoregulators than in the summer. In low thermal quality habitats, geckos sought rare, warm microclimates at night to maintain body temperatures warmer than most available environmental temperatures, and were highly effective thermoregulators. For ectotherms, appropriate environmental temperatures are a vital resource for survival, similar to food or shelter. The ability to exploit rare microclimates is especially important for nocturnal species, as heterogeneity of environmental temperatures is reduced at night compared to the day. In a warming world, it is vital to understand the thermal ecology of nocturnal ectotherms, as other species may shift to become more nocturnal to avoid lethal diurnal temperatures.

1. Introduction

Environmental temperatures (T_es) play a significant role in the behavior and physiology of all ectotherms, and studies of reptile thermal biology have been critical to our understanding of thermoregulation (Angilletta, 2009; Avery, 1982; Huey, 1982). Body temperature (T_b) regulation plays a vital role in the physiological functions of reptiles, including regulating metabolic function and growth (Autumn and DeNardo, 1995; Beaupre et al., 1993), digestion (Beaupre and Zaidan, 2012; Naulleau, 1983), locomotor performance (Bennett, 1990), and reproduction (Duvall and Graves, 1993; Schwarzkopf and Shine, 1991). Most studies have focused on diurnal (Grover, 1996; Klingenbock et al., 2000; Nordberg and Cobb, 2017, 2016; Stewart, 1965; Walguarnery et al., 2012; Wang and Adolph, 1995), rather than nocturnal groups (Aguilar and Cruz, 2010; Rock and Cree, 2008; Sievert and Hutchison, 1988; Webb and Shine, 2006). Whereas nocturnal species do not benefit directly from solar radiation, many studies have found nocturnal species thermoregulate behaviorally through conduction from the environment (e.g., warm rocks, buildings, trees; Kearney and Predavec, 2000; Schlesinger and Shine, 1994; Webb and Shine, 2006). In addition, many nocturnal reptiles thermoregulate during the day inside retreat sites, which may have significant impacts on their physiological performance (Bustard, 1967; Kearney and Predavec, 2000; Webb et al., 2004; Webb and Shine, 1998).

Thermal properties of the environment influence animal movement patterns, habitat selection, and territorial boundaries (Blouin-Demers and Weatherhead, 2001a, 2001b; DeGregorio et al., 2015a; Row and Blouin-Demers, 2006; Weatherhead et al., 2012). Whereas physical habitat features, such as structural complexity (Howland et al., 2014; Manning et al., 2013; Neilly et al., 2018) and connectivity (Baguette

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et al., 2013) are important drivers of diversity and richness, thermal habitat also influences species boundaries and distributions (Scheffers et al., 2017). Thus, the thermal environment is a key driver of many aspects of ectotherm resource use and behavior (Fitzgerald and Nelson, 2011; Huey, 1991; Huey et al., 1989).

Thermoregulation by nocturnal reptiles is generally constrained at night, because of the limited availability of suitable environmental temperatures (Angilletta et al., 1999; Huey and Slatkin, 1976). Preferred environmental temperatures may be available for only a short period of the day or season, forcing nocturnal species to acquire thermal energy during their 'inactive' times (i.e., during the day; Kearney and Predavec, 2000; Schlesinger and Shine, 1994). Reaching critical thermal thresholds is vital for essential functions like digestion, even in nocturnal species (Avery, 1982; Bustard, 1967). Diurnal and nocturnal species thermoregulate in slightly different ways: in hot, tropical regions, diurnal reptiles thermoregulate behaviorally to avoid overheating as environmental temperatures reach critical or lethal limits (Kearney et al., 2009; Vickers et al., 2011). In contrast, for nocturnal species, night time environmental temperatures are often lower than preferred temperatures, and therefore nocturnal species thermoregulate behaviorally to locate warm environmental microclimates within (or closer to) their preferred temperature range (Kearney and Predavec, 2000; Rock and Cree, 2008).

The bulk of the literature on the thermal ecology of nocturnal reptiles focuses on diurnal retreat site selection, and thermoregulation within retreat sites (Kearney, 2002; Schlesinger and Shine, 1994; Webb and Shine, 1998). Furthermore, many of these studies focus on species from arid (Angilletta et al., 1999; Angilletta and Werner, 1998; Lara-Reséndiz et al., 2015), temperate (Blouin-Demers and Weatherhead, 2001c; Brown and Weatherhead, 2000; Rock and Cree, 2008; Row and Blouin-Demers, 2006), or subtropical regions (Aguilar and Cruz, 2010; Huey and Pianka, 1977) characterized by low environmental temperatures at night, limiting the potential for thermoregulation to daytime hours. In contrast, the thermal ecology of tropical nocturnal reptiles has been examined much less often (Anderson et al., 2005). Tropical regions may provide nocturnal lizards more opportunities for thermoregulation at night, because environmental temperatures remain relatively warm. Given suitable environmental conditions, tropical nocturnal lizards may thermoregulate actively throughout the night, as well as in diurnal retreat sites.

In this study, our aim was to identify if, and to what extent, thermoregulation occurred at night during the active period of a tropical, predominantly nocturnally active lizard. Using temperature-sensitive radio transmitters, we quantified thermal selection of lizards in two seasons in a savanna woodland in the dry tropics of northeast Australia. By quantifying the availability of thermal resources using operative environmental temperature loggers, we aimed to determine if these lizards could exploit preferred microclimates at night when environmental temperatures were less heterogeneous.

2. Methods

2.1. Study species and area

This study was conducted at the Wambiana cattle station, a commercial cattle property located 70 km southwest of Charters Towers, in north Queensland, Australia. Wambiana station consists of open Eucalypt savanna woodlands, dominated by Reid River box (*Eucalyptus brownii*) and Silver-leaf ironbark (*Eucalyptus melanophloia*) trees. We used a locally abundant and widespread arboreal gecko, the Australian house gecko (*Gehyra dubia*), as our model organism to describe the thermal ecology of a tropical, nocturnal reptile. Native house geckos are nocturnal insectivores found on a variety of microhabitats including trees with flaking or peeling tree bark as well as urbanized microhabitats such as buildings (Nordberg et al., 2018; Nordberg and Schwarzkopf, 2019; Zozaya et al., 2015).

2.2. Thermal preference

To determine the preferred temperature ranges, we captured 29 geckos from Wambiana Station and brought them back to the laboratory at the James Cook University (JCU), Townsville, QLD. We measured the thermal preferences (T_{set}; Hertz et al., 1993) of all geckos (male: n = 11, non-gravid: n = 14 female, and gravid females: n = 4) in November of the pre-summer wet season. We placed geckos individually in multiple glass terraria (150 × 20 × 30 cm; L x W x H) in a controlled temperature room at JCU. The temperature gradient inside each of the glass chambers ranged from 6.5 to 40.0 °C, achieved by placing one end of each chamber on bricks sitting in ice water and a heat lamp placed under the opposing end of the chamber. The testing room had a constant air temperature of 25 °C with a 12:12 light-dark cycle. Each gecko was placed in a chamber for 2 h prior to recording T_bs. All terraria were cleaned with 70% ethanol between trials. Thermal images of each gecko were taken using a thermal camera (model EasIR-9, 384 × 288 pixels, Wuhan Guide Infrared Co., Ltd., China) every 2 h for the 24-h trial to acquire T_bs without disturbing the lizards by handling. To justify the use of thermal images to infer T_b, we used a subset of randomly selected T_b measurements (n = 20) and attained a cloacal temperature and a thermal image nearly simultaneously (within 5 s). Gecko T_bs estimated from the dorsum of each gecko via thermal images were highly correlated with cloacal temperature of the same gecko obtained simultaneously (n = 20 paired T_bs; Pearson's correlation: $t = 48.37$, $df = 18$, $p < 0.001$, $R^2 = 0.99$). We used the central 50% of observed T_bs for each gecko to determine the thermal preference (T_{set}; Christian and Weavers, 1996; Hertz et al., 1993). We calculated T_{set} for each individual, and then calculated the mean T_{set} among all individuals and among sex categories. All geckos were later maintained at JCU for additional studies.

2.3. Radio telemetry

We monitored the field T_bs of 15 geckos during the winter dry season (August 2015), and 11 geckos during the summer wet season (February 2016) over the course of 7 days (Table 1). Geckos were captured opportunistically during spotlight surveys at the beginning of each survey period. Only large adults (SVL = 57.3 ± 0.66; mass = 5.7 g ± 0.15) were used for transmitter attachment to ensure that the transmitter package did not exceed 5% of their body weight. We glued small, temperature-sensitive radio transmitters (Model LB-2XT, 0.22 g, 8 × 4x2.8 mm (LxWxH), battery life of ~7 days, Holohil Systems, Carp, Ontario, Canada) to a piece of rubber dialysis tubing and cotton thread to make 'waist-belt' transmitter packages (total weight ~ 0.26 g) for each gecko (Fig. 1). Each gecko was released at their tree of capture the following night and located four times per night (approximately every 4 h) for up to 7 days, and additionally, four times throughout the day in the dry season 2015. Geckos were not

Table 1
Mean and standard error measures for gecko snout-vent-length (SVL) and mass used in both the thermal gradient laboratory experiment and the field telemetry experiment.

Date	Group	Sex	n	SVL (mm)		Mass (g)	
				Mean	SE	Mean	SE
November 2016	Thermal gradient	Male	11	57.5	1.7	4.7	0.4
		Non-gravid	14	58.1	1.0	4.8	0.3
		Gravid	4	60.0	1.0	5.6	0.5
January 2016	Field	Male	3	57.7	2.7	5.6	0.1
		Non-gravid	3	53.7	0.9	5.4	0.3
		Gravid	5	60.0	1.3	5.9	0.3
August 2015	Field	Male	11	57.4	0.8	5.7	0.2
		Non-gravid	2	55.5	3.5	5.3	0.3
		Gravid	2	57.0	3.0	7.0	1.0

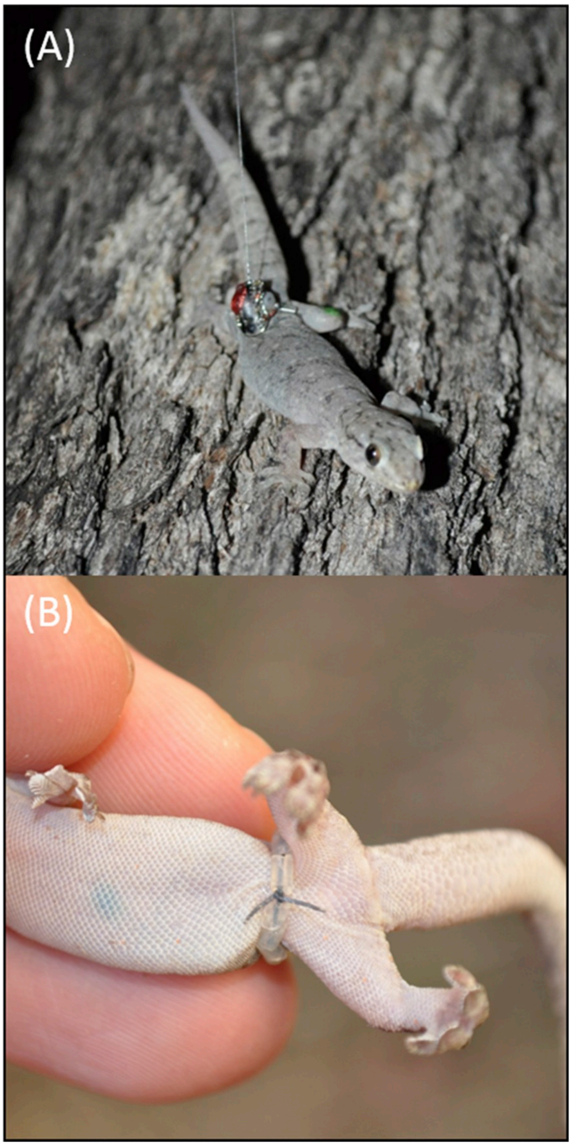

Fig. 1. Temperature-sensitive radio transmitter 'waist-belt' attachment to adult *Gehyra dubia*. Radio transmitters were fitted dorsally around the inguinal region (A) and attached with cotton thread fed through thin rubber dialysis tubing (B).

located during the day in the summer wet season due to limited site access and equipment failure.

2.4. Body temperature and indices of thermoregulation

We used temperature-sensitive radio transmitters to estimate the T_bs of free-ranging geckos. At each relocation, we recorded the time it took to accumulate 11 pulses (i.e., ten pulse intervals) to match with Holohil-supplied temperature calibration curves. We compared temperatures collected from the external transmitter waist-belt to internal cloacal temperatures at a variety of temperatures prior to releasing the gecko to determine the accuracy of measuring gecko T_bs (which were highly correlated $R^2 = 0.99$; see Appendix A.1, Fig A1 for details). In addition, during the dry season in 2015, we used an automated system to record pulse intervals to accumulate near-continuous T_bs (cycling through transmitter frequencies and recording T_bs every 1–2 min) throughout the sampling period (Lotek, SRX 400 Telemetry Receiver, Newmarket, Ontario) amassing a large amount of T_b data during the short lifespan of the transmitters.

Table 2
Measured indices of thermoregulation.

Index	Definition
T_b	Body temperature
T_e	Operative environmental temperature
T_{set}	Body temperature preference; central 50% of body temperatures selected in thermal gradient
d_b	Accuracy of thermoregulation, measured as (absolute) mean deviation of T_b from T_{set}
d_e	Thermal quality of the habitat, measured as (absolute) mean deviation of T_e from T_{set}
E	Effectiveness of thermoregulation; d_e - d_b

Adapted from Hertz et al. (1993).

We calculated multiple indices of thermoregulation (Table 2), developed by Hertz et al., (1993), who specify the importance of identifying the extent to which animals maintained T_bs within T_{set} in relation to how often the available T_e fell within T_{set}. These calculations and our interpretation of the results follow the assumption that gecko T_{set} does not change seasonally, as we have only conducted the thermal gradient experiment one time. We calculated the accuracy with which T_bs were maintained (d_b; Hertz et al., 1993), represented by the absolute mean deviation in T_bs from T_{set}. If T_bs were greater than T_{set}, d_b was calculated as the mean deviation in T_bs from the upper bound of T_{set}, and if T_bs were less than T_{set}, d_b was calculated as the mean deviation in T_bs from the lower bound of T_{set}. Similar to d_b, we also calculated the mean deviation (absolute value) of T_es compared to T_{set} temperatures, producing the index d_e. We then used both d_b and d_e to calculate the effectiveness of thermoregulation (E) as the difference between d_e and d_b, or the extent to which T_{set} was maintained in the face of thermal variation in the environment (Blouin-Demers and Weatherhead, 2001a). Values near 1 indicated high effectiveness of thermoregulation, near zero values represent thermoconformity, and negative values represent animals that avoid thermally favorable microhabitats. Additionally, we assessed the response of geckos to varying thermal quality in different seasons, and regressed effectiveness of thermoregulation (E or d_e-d_b) on d_e (Blouin-Demers and Nadeau, 2005; Row and Blouin-Demers, 2006; Vickers et al., 2011). The relationship of d_e and d_b in a thermoconformer would have a slope of 1, where a slope < 1 indicates an animal's effectiveness of thermoregulation increases as the thermal quality of the habitat decreases. Conversely, a slope of > 1 indicates an animal's effectiveness of thermoregulation decreases when the thermal quality of the environment decreases.

2.5. Operative temperatures and environmental thermal quality

We used operative temperature models to measure the available environmental temperature (T_e) across five microhabitats used by geckos in both the dry and wet season. Operative models consisted of temperature data loggers (DS1925, Thermochron iButtons, Maxim, Dallas, TX) placed inside a small, off-white cloth bag. We compared cloth models to more traditional copper operative models and found copper models were not significantly better predictors of gecko T_bs (Appendix A.1), therefore we used cloth models as they could be more easily placed in small microhabitats (Vickers and Schwarzkopf, 2016a, 2016b). Models were calibrated by placing a model in direct sunlight (despite most of our models were to be placed in hollows and under tree bark where they would not be exposed to solar radiation) next to a recently deceased gecko carcass with a temperature logger placed inside the body cavity, recording temperatures every 5 min for approximately 24-h. We plotted the temperatures estimated by our operative models versus those obtained from the gecko carcass, and found temperatures to be highly correlated ($R^2 = 0.97$; Appendix A.1, Fig A2). The operative models were very slightly but significantly warmer than the gecko carcass (paired t-test: $t_{1,259} = 5.667$, $P < 0.001$; mean difference = 0.16 °C), although, the differences in temperatures were negligible due to the error of the temperature loggers (± 1 °C), and therefore were ignored in further analyses (Row and Blouin-Demers, 2006). Sixty operative models were placed throughout the environment, 12 in each microhabitat: under loose tree bark, on top of tree bark, 2-m above the ground in shaded open air 10 cm from the tree trunk, in hollows or logs, and on the ground. Operative models recorded T_e every hour for the duration of the sample period (~ 7 days).

2.6. Statistical analyses

We compared the thermal preference of geckos in a laboratory thermal gradient from three sex categories (males, non-gravid females, and gravid females) using linear mixed-effects models (*lme4*, Bates et al., 2014) with body temperature as our dependent variable, sex category as a fixed effect, and gecko ID as a random factor. We conducted post-hoc pairwise comparisons (*lsmeans*, Lenth, 2016) to identify which sex categories differed from each other. Similarly, we compared the T_bs of free ranging geckos using linear mixed-effects model and subsequent post-hoc pairwise comparisons to identify potential differences in T_bs of geckos between seasons and sex categories (fixed effects) and gecko ID as a random factor. We tested the effects of season and time of day (day vs. night) on the deviation in T_bs from T_{set} (d_b) using a linear mixed-effects model. Season and time of day were fixed effects and gecko ID was used as a random factor. A similar model was used to test the effects of season and time of day on the effectiveness of thermoregulation (E or $d_e - d_b$). We used linear regression to identify if geckos more closely resembled thermoregulators or thermoconformers by regressing the accuracy of T_b (d_b) against the thermal quality of the habitat (d_e). We then compared the slope of the line of each season to each other and compared to a slope of 1 using a series of three t-tests and Bonferroni adjusted p-values (see section 2.4 for details). All statistical analyses were performed in the program R (version 3.4.3, R Core Team, 2017). We inspected residual boxplots and determined if the assumptions of normality and homogeneity of variance were met and transformed data where required. Means are presented as ± 1 SE.

3. Results

3.1. Thermal preference

Overall, the mean T_{set} for all individuals was between 31.4 ± 0.59–34.5 ± 0.55 °C (Table 3). Geckos in different sex categories showed different thermal preferences (linear mixed-effects model: $F_{2,26} = 11.402$, $P < 0.001$; Fig. 2). Gravid females (mode = 29.9 °C) had significantly lower mean T_bs than males (mode = 31.1 °C; *lsmeans* post-hoc comparison: P = 0.014) and non-gravid females (mode = 35.5 °C; *lsmeans* post-hoc comparison: $P < 0.001$), but male and non-gravid females showed no significant difference (*lsmeans* post-hoc comparison: $P < 0.087$).

Table 3
Middle 50% quartile (25–75%) temperature preferences (T_{set}) of Australian native house geckos (*Gehyra dubia*) in a laboratory thermal gradient. The thermal gradient experiment was conducted in November 2016.

Sex Category	n	T_{set} range
		Temperature °C (mean ± SE)
Male	11	30.9 ± 1.04–34.2 ± 1.00
Non-gravid female	14	31.8 ± 0.71–34.7 ± 0.66
Gravid female	4	27.5 ± 0.45–30.1 ± 0.46
Total	29	31.4 ± 0.59–34.5 ± 0.55

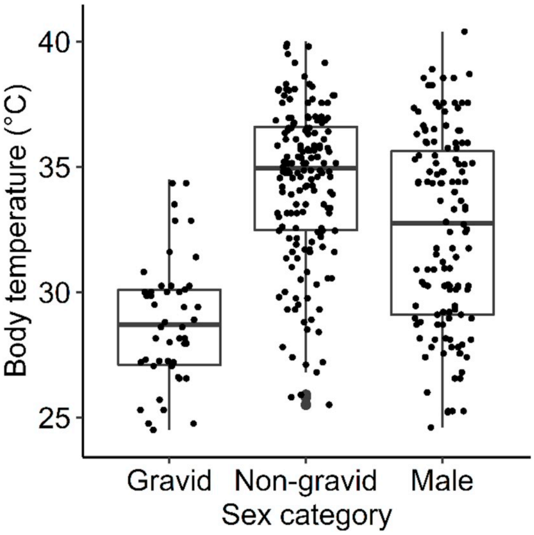

Fig. 2. Body temperatures of 11 male, 14 non-gravid female, and 4 gravid female *Gehyra dubia* in a laboratory thermal gradient. Gravid females selected significantly lower mean body temperatures than non-gravid females and males (*lsmeans* post-hoc comparison: male vs. gravid P = 0.014; non-gravid vs. gravid $P < 0.001$; male vs. non-gravid P = 0.087).

3.2. Field body temperatures

A total of 2065 T_bs were collected from temperature-sensitive radio transmitters (dry season = 1660 T_bs; wet season 405 T_bs). Gecko T_bs were significantly warmer in the wet season than the dry season (linear mixed-effects model: $F_{1,26} = 5.738$, P = 0.024), but we found no difference in the T_bs of geckos among sex categories (linear mixed-effects model: $F_{2,24} = 0.626$, P = 0.543).

3.3. Operative environmental temperatures

We recorded a total of 11,096 T_es in the dry season and 10,372 T_es in the wet season from our operative temperature models. As expected, T_es were higher during the summer wet season (2016) than the winter dry season (2015). Only a small proportion of T_es fell within T_{set} in either season, especially at night when geckos were active (Table 4). Despite our efforts to capture the full range of T_es by deploying 60

Table 4
Proportion of available environmental temperatures (T_e) and gecko body temperatures (T_b) below, within, and above the preferred temperature range (T_{set} = 31.4–34.5 °C) of *Gehyra dubia* and the environmental maximum temperatures (T_{eMax}) measured from operative models.

Season	Time	n	T_e Below T_{set} (%)	T_e Within T_{set} (%)	T_e Above T_{set} (%)
Dry	Day	5461	68	17	15
	Night	5635	100	0	0
Wet	Day	5475	45	24	31
	Night	4897	97	3	0
			T_b Below T_{set} (%)	T_b Within T_{set} (%)	T_b Above T_{set} (%)
Dry	Day	811	52	31	17
	Night	849	98	2	0
Wet	Day	90	100	0	0
	Night	315	94	6	0
			T_b Below T_{eMax} (%)	T_b Above T_{eMax} (%)	
Dry	Day	811	87	13	
	Night	849	18	82	
Wet	Day	90	70	30	
	Night	315	60	40	

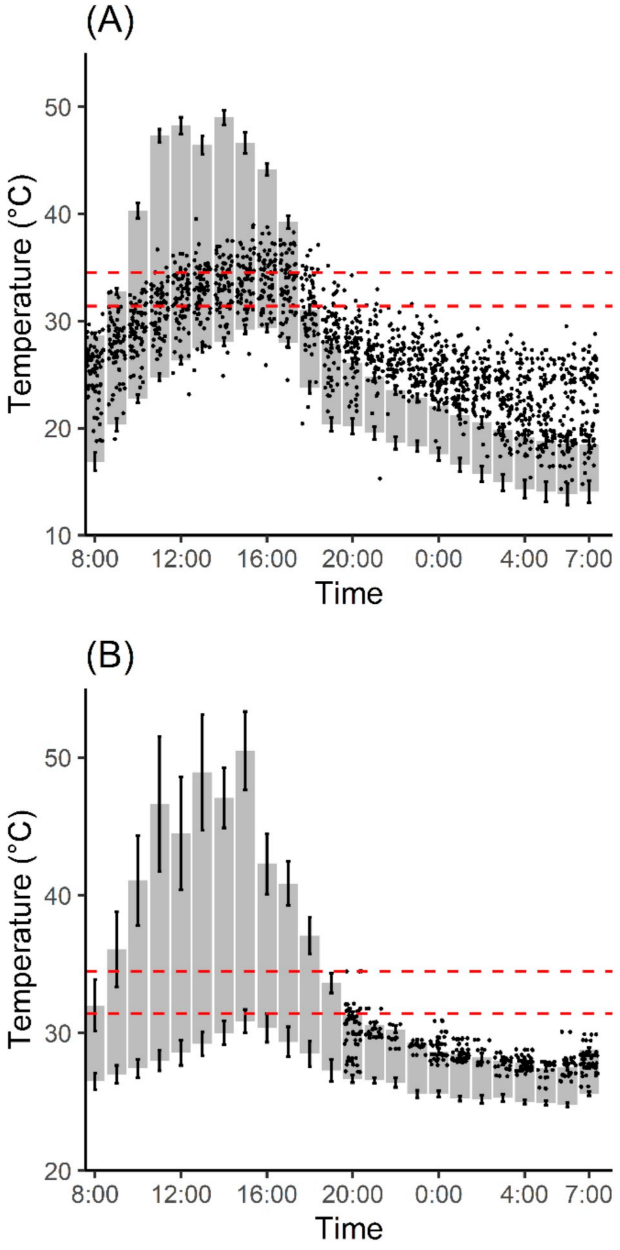

Fig. 3. Distribution of available environmental temperatures (grey bars = T_{eMin} – T_{eMax} ± 95% CI for daily variation) and gecko body temperatures (T_bs; points). Horizontal red dashed line indicates the preferred temperature (T_{set}) range of *Gehyra dubia* based on lab trials in a thermal gradient. Data presented from the winter dry season (August 2015; "A") and the summer wet season (February 2016; "B"). Diurnal temperatures were not recorded in the summer wet season due to limited site access and equipment failure.

operative models in a range of microhabitats, mean gecko T_bs remained above available T_es assessed by models at night in both seasons (mean ± SE deviation above maximum available T_es; dry season = 2.38 °C ± 0.08; wet season = −0.05 °C ± 0.05; Fig. 3). Further, eighty-two percent of gecko T_bs remained above the environmental maximum temperature (T_{eMax}) at night during the winter dry season, when T_es were coldest.

3.4. Effectiveness of thermoregulation

Native house geckos were able to maintain average T_bs above operative temperatures in both seasons (dry season: T_bs were on average 5.2 °C warmer than operative temperatures; wet season: T_bs were 1.3 °C warmer than operative temperatures). We found a significant season x time (day vs. night) interaction in the deviation in T_bs from T_{set} (d_b) with greater deviation during the day time and in the winter dry season (linear mixed-effects model: $F_{1,2041} = 208.5$, $P < 0.001$; mean ± SE, d_b dry.day = −2.00 °C ± 0.12; dry.night = −6.69 °C ± 0.11; wet.day = −3.52 °C ± 0.09; wet.night = −2.53 °C ± 0.14). Similarly, based on mean deviations of T_bs from T_{set} relative to environmental temperatures (*E*), geckos were more effective thermoregulators in the dry season than the wet season, especially at night (linear mixed-effects model: $F_{1,2041} = 114.08$, $P < 0.001$; mean ± SE, *E* dry.day = 1.40 °C ± 0.09; dry.night = 4.89 °C ± 0.09; wet.day = 1.30 °C ± 0.09; wet.night = 1.47 °C ± 0.03). In the dry season, geckos were more effective thermoregulators when the thermal quality of the habitat was low compared to the wet season (Fig. 4). In both seasons, at night, geckos more closely resembled thermoregulators than thermoconformers (slopes were significantly different from 1, Blouin-Demers and Nadeau, 2005, Fig. 4), and were different from each other (one sample t-test: all Bonferroni adjusted P values < 0.001). Geckos were more effective thermoregulators at night, especially in the dry season when environmental temperatures were furthest from T_{set} (Fig. 5).

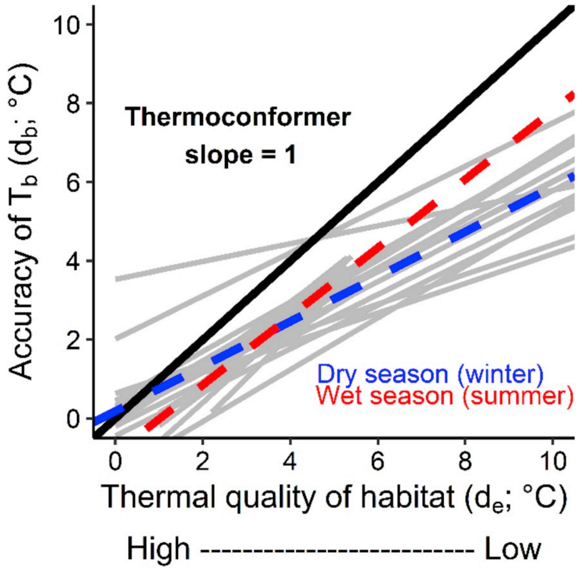

Fig. 4. Mean accuracy of thermoregulation (d_b) and thermal quality of the habitat (d_e) for *Gehyra dubia* in the dry season (winter; blue) and wet season (summer; red). Grey solid lines represent individual geckos, the dashed lines represent the mean slope for each season. The solid black line indicates m = 1; or thermoconformity; Blouin-Demers and Nadeau (2005); Row and Blouin-Demers (2006); Vickers et al., (2011).

4. Discussion

While male and non-gravid female geckos showed no difference in T_{set} in the thermal gradient, gravid females selected lower temperatures. This could have been due to a small sample size (n = 4), or because gravid females may prefer body temperatures different from those of males or non-gravid females (e.g., Schwarzkopf and Shine, 1991). Interestingly though, we found gravid geckos to select lower temperatures rather than warmer temperatures, in contrast to other studies (Dayananda et al., 2017; Schwarzkopf and Shine, 1991). Although outside the scope of this study, it would be beneficial to identify if T_{set} shifts seasonally, and increase the sample size of gravid females to identify if they continue to select lower temperatures than non-gravid and male geckos.

The thermal quality of the habitat fluctuated seasonally, with higher thermal quality in the wet season, when there were smaller deviations between T_es and T_{set}. In our study, geckos were significantly more

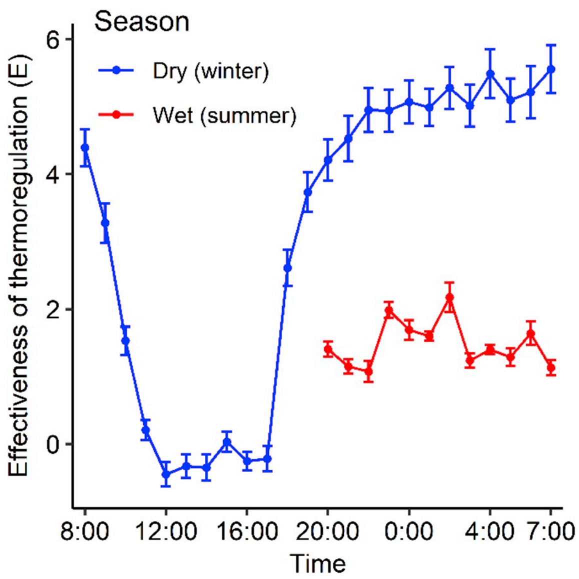

Fig. 5. Daily variation in hourly (mean ± SE) measures of effectiveness of thermoregulation (*E*) in *Gehyra dubia* in the dry season and wet season. Values near zero represent thermoconformity, positive values represent effective thermoregulation.

effective thermoregulators at night in the dry season than the wet season. Dry season T_es were cooler, and had greater deviations from T_{set}, therefore geckos had to seek out rare, suitable T_es to thermoregulate. Throughout the day, geckos thermoregulated less effectively, except in the early morning and late evening. When the thermal quality of the habitat was low, geckos increased the effectiveness of thermoregulation to make up for suboptimal thermal quality, a phenomenon which occurs in both temperate (Blouin-Demers and Nadeau, 2005; Row and Blouin-Demers, 2006) and tropical regions (Vickers et al., 2011) in diurnal reptile groups.

Native house geckos found rare microclimates at night and used them to thermoregulate behaviorally, despite their limited availability. Thermoregulating at night allowed geckos to keep their body temperature on average 1.3 °C above operative temperatures in the wet season, and 5.2 °C in the dry season. *Gehyra dubia*, although nocturnal, and therefore supposedly limited to an environment in which the opportunities for thermoregulation were limited, had high thermal preferences, higher than many other arboreal nocturnal geckos (*Gehyra dubia*: preferred mean body temperature (PBT) = 32.9 °C ± 0.2, T_{set} = 31.4–34.5 °C, this study; *Hemidactylus turcicus*: PBT = 28.4 °C ± 1.5, *Oedura reticulata*: PBT = 31.2 °C ± 0.8, Angilletta et al., 1999; *Christinus marmoratus*: T_{set} = 23.6–26.0 °C, Kearney and Predavec, 2000; also see Bustard, 1967; Light et al., 1966). High thermal preferences are consistent with their tropical distribution, and is also common among species in the genus *Gehyra* (Angilletta et al., 1999; Froudist, 1970; Light et al., 1966). Given the opportunity (i.e., in the lab), geckos selected high temperatures throughout the day and night. In the field, only a small proportion of T_es fell within T_{set}, especially at night when geckos were most active (Table 4), but geckos managed to stay warmer than operative temperatures for much of the night, even under these conditions.

A reduction in effectiveness of thermoregulation likely has associated costs, such as increased predation risk due to conspicuousness (Webb and Whiting, 2005), reduced foraging time (Downes, 2001), or a reduction in the ability to defend territories (Downes and Shine, 1998). We occasionally observed geckos basking in early morning sunlight on the sides of loose, peeling tree bark (Bustard, 1967; Kearney, 2002; Webb and Shine, 1998) and had two geckos depredated by Pied Butcherbirds (*Cracticus nigrogularis*), and impaled on dead branches during the study. These individuals were likely depredated while basking, or dislodged from their diurnal retreat site in the early morning when butcherbirds were foraging. Ectotherms have to balance the trade-offs between thermoregulation and thermorconformity, both of which have costs and benefits (Huey and Slatkin, 1976). The costs can be lethal, not only in terms of predation, but also thermally, in which forgoing thermoregulation can expose animals to extreme or even lethal T_bs, especially in thermally extreme environments. To minimize the risk of predation, many nocturnal reptiles thermoregulate in diurnal retreat sites, which often provide more diverse microclimates for thermoregulation than microclimates they encounter while active at night (Bakken, 1992; Kearney and Predavec, 2000; Webb and Shine, 1998).

Previous studies quantifying the thermal environment were often limited by the number and capacity of operative models (Blouin-Demers and Weatherhead, 2001c; Shine et al., 2003; 2 and 6 models respectively), or the number of models used were not reported (Brown and Weatherhead, 2000; Cobb and Peterson, 2008; Wills and Beaupre, 2000), but advances in temperature recording technology has made obtaining temperature data relatively cheap and easy. In our study, we deployed 60 iButton temperature loggers, placing 12 replicate loggers in five different microhabitats recording temperatures every hour to try and accurately characterize the thermal environment to which geckos were exposed. To our surprise, gecko T_bs were often higher than even our T_{eMax} for the site (Fig. 3). Initially, we thought that maybe the transmitters or temperature loggers were not working properly, but that was not the case (see calibrations in text above). In our attempts to describe this phenomenon, we examined relocations of geckos when they were visible during radio telemetry, and in many cases, the deviation of T_bs to T_{eMax} was lowest when geckos were visible (i.e., they were in the environments we were sampling with our temperature loggers, Appendix A.1; Fig. A3). This suggests that while the T_bs of geckos were generally higher than most T_es, (presumably as they shuttled in and out of rare, warm microclimates), when geckos were visible, they more closely matched our T_es from operative models. Thus, we strongly suspect geckos are extremely good at seeking out rare thermal microclimates that retain higher T_es throughout the night.

Native house geckos are crevice-dwellers, and easily slip in and out of very tight spaces in cracking tree bark and hollows (Nordberg and Schwarzkopf, 2019; Wilson, 2015). We suspect that geckos were exploiting thermal microclimates that were not easily available to sample with temperature loggers (e.g., in deep bark fissures, or hollow branches). Trees are complex structures, providing a complex thermal environment and varying available environmental temperatures. Depending on various characteristics, such as bark color, structure, and sun exposure, trees can retain thermal inertia for multiple hours after sunset (Coombs et al., 2010; Nicolai, 1986). We suspect that geckos were seeking out these warm microclimates and achieved warmer T_bs than most T_es. While few studies have directly measured thermoregulation of nocturnal lizards using thermal indices, Gourett (2016) showed a similar pattern, with nocturnal leaf-tailed geckos (*Saltuarius cornutus*) exhibiting higher T_bs than ambient T_es in wet tropical rainforests of northern Australia. Similarly, Weatherhead et al. (2012), found mean rat snake (*Elaphe [Pantherophis] obsoleta*) T_bs that were higher than T_{eMax} at night for three populations in Texas, Illinois (USA), and Ontario (CA), suggesting that rat snakes can seek out rare microclimates that are presumably not easily sampled.

Nocturnal and diurnal ectotherms face similar challenges with respect to thermoregulation. Diurnal lizards, especially in extreme environments, are forced to thermoregulate to avoid lethally high T_es (Vickers et al., 2011). In contrast, nocturnal lizards often thermoregulate to seek out rare warm environments, avoiding cooler T_es, not suitable for maintaining physiological functions. For ectotherms, temperature is an extremely important resource, and should be viewed as such (Magnuson et al., 1979). Further, rare thermal niches are exploited and selected for, similar to other desired resources like food or microhabitats.

Environmental temperatures are an important driver of behavior and physiological function in ectotherms, regardless of their activity times (e.g. nocturnal vs. diurnal). A large proportion of the world's animals are nocturnal, including both endotherms (e.g., Bennie et al., 2014), and ectotherms (e.g., Hoskin et al., 2015; Meiri, 2018), yet nocturnal groups are comparatively underrepresented in the literature, especially in the context of their thermal ecology. With the onset of climate change and a global increase in environmental temperatures, we may see shifts in species activity times to avoid lethal exposure to high temperatures (DeGregorio et al., 2015b, 2015a; Kearney et al., 2009). With a clear understanding of how ectotherms attain preferred temperatures and maintain physiological function in a thermally challenging world, we can better predict how other species may behave and perform in a thermally extreme future.

Authors' contributions

EJN and LS conceived the project idea and designed methodology; EJN collected and analyzed data and led the writing of the manuscript. EJN and LS both contributed critically to drafts and gave final approval for publication.

Data accessibility

Data available via the Dryad Digital Repository XXXXX.

Conflicts of interest

There are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.03.018.

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