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RESEARCH ARTICLE

Too cold is better than too hot: Preferred temperatures and basking behaviour in a tropical freshwater turtle

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Abstract

Thermoregulation is critical to the survival of animals. Tropical environments can be particularly thermally challenging as they reach very high, even lethal, temperatures. The thermoregulatory responses of tropical freshwater turtles to these challenges are poorly known. One common thermoregulatory behaviour is diurnal basking, which, for many species, facilitates heat gain. Recently, however, a north-eastern Australian population of Krefft's river turtles (*Emydura macquarii krefftii*) has been observed basking nocturnally, possibly to allow cooling. To test this, we determined the thermal preference (central 50% of temperatures selected) of *E. m. krefftii* in an aquatic thermal gradient in the laboratory. We then conducted a manipulative experiment to test the effects of water temperatures, both lower and higher than preferred temperature, on diurnal and nocturnal basking. The preferred temperature range fell between 25.3°C (±SD: 1.5) and 27.6°C (±1.4) during the day, and 25.3°C (±2.4) and 26.8°C (±2.5) at night. Based on this, we exposed turtles to three 24 h water temperature treatments ('cool' [23°C], 'preferred' [26°C] and 'warm' [29°C]) while air temperature remained constant at 26°C. Turtles basked more frequently and for longer periods during both the day and night when water temperatures were above their preferred range (the 'warm' treatment). This population frequently encounters aquatic temperatures above the preferred thermal range, and our results support the hypothesis that nocturnal basking is a mechanism for escaping unfavourably warm water. Targeted field studies would be a valuable next step in understanding the seasonal scope of this behaviour in a natural environment.

KEYWORDS
Australia, ectotherm, nocturnal basking, thermoregulation, thermoregulatory cooling

INTRODUCTION

Behavioural thermoregulation in ectotherms evolved to satisfy physiological requirements by exploiting thermally diverse microhabitats (Angilletta, 2009; Huey & Bennett, 1987; Meek & Avery, 1988). Reptiles maintain body temperatures within their preferred range (T_{set}) by moving between a heat source, such as a sunny area, and a heat sink, like shade or cool water. Movement between warm and cool locations is common among diurnal, heliothermic reptiles that rely on solar radiation as their primary source of heat (Avery, 1982; Christian & Weavers, 1996; Meek, 1995; Seebacher & Grigg, 1997).

In freshwater turtles, diurnal basking is common (Boyer, 1965) and enables heat gain via absorption of solar radiation (Cowles & Bogert, 1944). This provides several benefits, such as elevating body temperatures to enhance food consumption and digestion (Gatten, 1974; Kepenis & McManus, 1974;

Parmenter, 1980; Spencer et al., 1998) and increasing metabolic rates for growth and reproduction (Bulté & Blouin-Demers, 2010a). Additionally, basking may aid absorption of ultraviolet rays for vitamin D synthesis (Acierno et al., 2006), dry the skin and shell to assist in ecdysis, prevent algal infections (Neil & Allen, 1954) and reduce body burdens of leeches (McCoy et al., 2007, but see Readel et al., 2008 and McKnight et al., 2021). However, empirical evidence to validate non-thermoregulatory basking functions, such as parasite removal, is limited, and patterns of diurnal basking are strongly associated with environmental conditions that facilitate body temperature optimization (Boyer, 1965; Clavijo-Baquet & Magnone, 2017; Crawford et al., 1983; Ernst, 1982; Graham & Hutchison, 1979; Obbard & Brooks, 1979; Schwarzkopf & Brooks, 1985).

In an intriguing exception to the standard basking behaviour outlined above, several tropical and subtropical turtle species, including Krefft's river turtles (*Emydura macquarii krefftii*) from north-eastern Australia (Townsville, Queensland), have recently been documented emerging from the water to 'bask' nocturnally (Nordberg and McKnight, 2020; McKnight et al., 2023). Thermoregulation by reptiles at night is thought to be constrained by both low environmental temperatures and low thermal heterogeneity (Hitchcock & McBrayer, 2006; Kearney & Predavec, 2000). However, in tropical systems, environmental temperatures may remain high, even at night (Nordberg and McKnight, 2023), and some nocturnal reptiles can thermoregulate through shifts in microclimates (Nordberg & Schwarzkopf, 2019) or simply conform to high-quality ambient temperatures (Arenas-Moreno et al., 2018; Shine & Madsen, 1996).

Conversely, several studies have documented the need for tropical reptiles to lose heat more generally, because of the fitness costs associated with further elevating body temperatures in warm environments (Deutsch et al., 2008; Huey et al., 2009, 2012; Kearney et al., 2009; Tewksbury et al., 2008; Vickers et al., 2011). The asymmetric thermal performance curves typical of reptiles drive rapid declines in fitness for equal shifts in body temperature above the thermal optimum compared with below optimum by a similar magnitude (i.e. 'Jensen's inequality' in thermal performance curves; Martin & Huey, 2008). Thus, heat avoidance may be an important component of *E. m. krefftii*'s thermoregulatory behaviour.

In northern Queensland, elevated water temperatures may persist well into the night. Indeed, local water temperatures for this population may exceed 30°C on summer evenings (Nordberg and McKnight, 2023), which raises the possibility that *E. m. krefftii* in Townsville bask nocturnally to avoid the heat. To test this hypothesis, we first determined the preferred temperature range of *E. m. krefftii*. We then conducted a manipulative basking choice experiment, in which we allowed turtles to choose whether or not to bask under different thermal scenarios. We hypothesized that turtles would avoid both high and low temperatures and select temperatures within their preferred range by basking.

METHODOLOGY

Study site

This study was conducted at the James Cook University campus in Townsville, tropical north Queensland, Australia. Turtles were captured from the Ross River (19°18′33″ S 146°45′57″ E), which flows through Townsville and is bordered by *Melaleuca* spp. and *Eucalyptus* spp. trees, grass, logs and aquatic vegetation. One side of the river is largely bushland, but the other is heavily developed for community use, and includes houses and lawns, piers, boat ramps and pedestrian bridges. The main channel is up to 150 m wide, and *Emydura macquarii krefftii* are locally abundant.

Thermal preference study

Twenty-two adult, male *E. m. krefftii* were captured from the Ross River in the austral summer, between late November 2021 and mid-January 2022, using sardine-baited cathedral nets. Cathedral nets were suspended overnight at a depth of ~1–2 m and collected the following morning. Captured turtles were housed individually in containers filled with dechlorinated freshwater and kept in a temperature-controlled laboratory (air temperature 26°C ± 1°C) at the Marine and Aquaculture Research Facility at James Cook University, Townsville. The laboratory was equipped with an automated 13:11 light: dark cycle that simulated natural light conditions at the time of the study (light from 05:30 to 18:30). Straight carapace length, mass and total number of leeches per individual were recorded before trials were conducted.

Thermal gradients

Two identical aquatic thermal gradients were constructed, each 210 × 70 × 51 cm, 1 m apart. Water depth was 15 cm throughout each tank. The tanks had alternate directions of heat flow, such that the hot end of one tank aligned with the cold end of the other, and each contained six partial, vertical barriers (45 × 1 × 15 cm; Figure 1). Barriers were spaced 31 cm apart, perpendicular to the tank walls, in an alternating pattern that allowed turtles to move freely along a meandering path. The barriers were critical to partition the flow of water and prevent rapid mixing of warm and cool currents. To establish a thermal gradient, warm (34°C) and cool (20°C) water

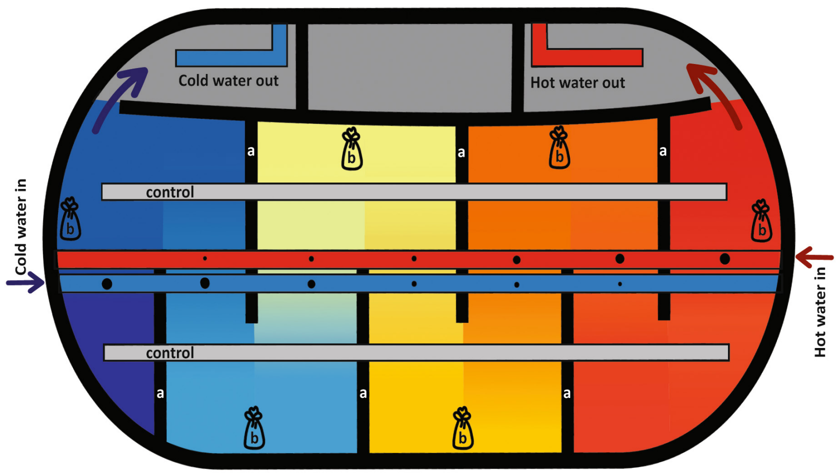

FIGURE 1 Diagram of aquatic thermal gradient used to measure preferred temperatures of *Emydura macquarii krefftii*. Pictured are the tank's partial barriers (a), the location of the iButton temperature loggers (which are distributed among six bags, with bags at the hot and cold extreme of the tank containing two iButtons each; b), and the control pipes ('control'). Hot- and cold-water inlet (middle of the tank) and outlet pipes (wall of the tank) are represented in red and blue, respectively. Arrows represent the direction of water inflow (straight) and outflow (curved) for hot and cold water. The outlet pipes were isolated from each other and from the rest of the arena by barriers. The temperature throughout the tank is represented in a heatmap gradient ranging from cold (blue) to hot (red). For thermal image of the gradient, see Figure S1.

was slowly, but continuously, delivered to opposite ends of each tank. This was achieved by using separate inflow pipes for warm and cool water. Each pipe originated at opposite ends of a tank and ran centrally down the tank, above the barriers, with a row of downward-facing holes. The holes decreased in size (10–2.5 mm) as they moved away from the inlet point. In this way, each partial tank section received a different proportion of warm and cool water, with one end receiving only warm water, the next section receiving mostly warm and some cool water, and so on.

To ensure that turtles would not bias their selected temperatures by using the inlet pipes as hides, additional 'control' pipes (with no water flow) were placed evenly between both sides of the functioning pipes and the walls of the tanks (Figure 1). Water exited the tanks via outflow pipes on the cold and hot ends of the tanks, each of which returned water to a sump tank with either a TAC250 Toyesi aquatic chilling pump or heaters (a series of model E01A08 heating elements), respectively. This slow, constantly flowing system established continuous thermal gradients spanning ~20–31°C. Water temperature in each gradient was measured continuously using an array of eight iButton temperature loggers (Thermochron TC DS1921G, two iButtons for the 'hot' and 'cold' end of each tank and one iButton for each of the four intermediate 'chambers' between barriers; Figure 1) treated with a water-resistant coating (PlastiDip™). Each iButton recorded water temperature every 15 min to ensure that the gradients maintained stable temperatures throughout the trials.

Each turtle was housed in the thermal gradient arena for a period of 24 h to allow them to acclimate, prior to a 24 h testing and data collection period. Each turtle's selected temperatures were recorded every 2 min using four iButtons temporarily attached to the anterior and posterior left and right carapace with cyanoacrylate glue. The mean temperature recorded by all four iButtons in each two-minute interval was used for analyses. To examine diel variation, day and night temperature selection was examined separately. Summary statistics (mean, median, mode and standard deviation) of the selected temperatures of each *E. m. krefftii* were calculated for each testing period (i.e. day and night). For each individual, the central 50% of selected temperatures (i.e. the median selected temperature bounded by the interquartile range: T_{set}) for diurnal and nocturnal trial periods was calculated. These values were averaged across individuals to determine the thermal preference for the sample population as is standard (Christian et al., 2016; Hertz et al., 1993). One individual had a bimodal distribution of body temperatures (i.e. there were two different temperatures that were selected with maximum, yet exactly equal frequency). Therefore, for the population mode, those two modes were averaged to provide a single value before being averaged with the other individuals' modes.

Manipulative basking experiment study

A new group of 31 adult *E. m. krefftii* (28 males and three females) were captured from the Ross River between April and May 2022 using baited cathedral nets. Turtles were housed individually for a maximum of 4 days before beginning the experiment.

Basking arenas

All trials were conducted in one of the two identical tanks (same dimensions as aquatic thermal gradients described previously), which were subdivided using two lightweight plastic (Corflute™, Corex Plastics) barriers (height = 45 cm) such that each tank contained three isolated chambers of roughly equal size (Figure 2). This set-up was similar to the thermal gradient, except water was delivered to each chamber via a perforated pipe along the centre bottom of the tanks, and only one temperature was delivered at time. Each barrier contained a series of small holes along the base so that water could pass between chambers. Water exited the tanks through a single outlet and was returned to a single sump tank with a TAC250 Toyesi aquatic heating/chilling pump which was used to set and maintain the desired temperature. Each chamber contained a single basking platform, ~1–2 cm above the water's surface, and fitted with a ramp to facilitate basking. A wildlife camera (CamPark T85™) was suspended above each chamber, 1 m above the basking platform, and set to time-lapse mode, taking photographs every 2 min with an infrared flash.

To test for thermal effects on basking behaviour, turtles were exposed to three water temperature treatments ('cool' [23°C], 'preferred' [26°C] and 'warm' [29°C]). Treatment temperatures were based on the extremes of the nocturnal preferred temperature range for this population (25.3°C ± 2.4 to 26.8°C ± 2.5) measured previously. We selected the nocturnal thermal preferences because we were primarily interested in nocturnal basking behaviour; however, the preferred temperature ranges were similar during the day and night (see Results). Water and air temperatures for the tanks were measured at 15 min intervals using iButton temperature loggers (Thermochron TC DS1921G) treated with a water-resistant coating (PlastiDip™) to ensure temperatures remained stable throughout all trials. Air temperatures on the basking platforms varied slightly and unavoidably from the set temperature (26°C) due to the thermal inertia of the tanks; however, they always remained within *E. m. krefftii*'s thermal preference range (total mean = 26.12°C ± SD: 2.29). Mean (±SD) air temperatures during each trial were as follows: warm = 26.16°C (±0.16), preferred = 25.40°C (±0.25) and cool = 24.76°C (±0.22).

Each turtle was tested individually in a separate compartment of the testing arena, with 1–6 turtles tested simultaneously (i.e. a 'batch' of turtles was distributed among isolated compartments in one of the two testing arenas; one turtle per compartment; Figure 2). Each trial lasted 4 days, including a day and night of acclimation (24 h) at 26°C, followed by three consecutive days and nights in which turtles were exposed to each water temperature treatment. Treatment order was randomized for each batch of turtles. Each day, 30 min were required for turtle husbandry, such as siphoning waste,

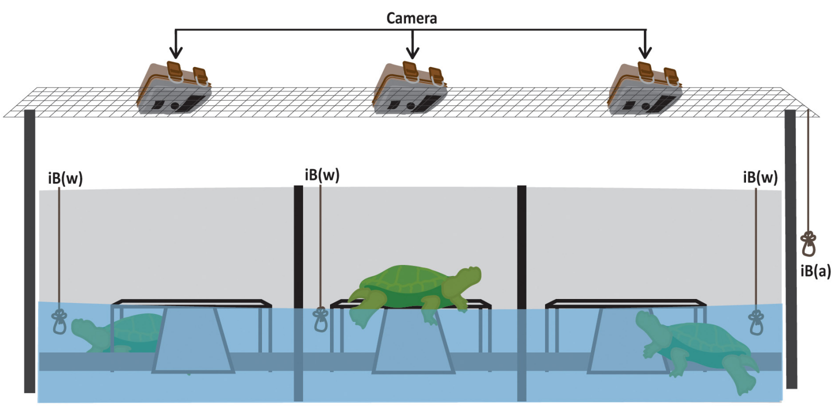

FIGURE 2 Testing arena (side view) used for *Emydura macquarii krefftii* basking experiment. Tanks were subdivided into three individual chambers (one turtle per chamber), each containing a single basking platform fitted with a ramp. A wildlife camera was suspended directly above the basking platform in each chamber. iButton temperature loggers were used to record air ('iB(a)') and water ('iB(w)') temperatures.

and manually setting new treatment temperatures (the system took 30 min to establish a new water temperature throughout the tanks). To minimize disturbance to the turtles, cleaning and tank maintenance always occurred between 16:00 and 18:30 h, but turtles were otherwise undisturbed (no one entered the room during trials).

Wildlife cameras were used to document the duration of individual turtle basking events using time-lapse photographs. We defined basking as any instance in which a turtle emerged from the water with more than two-thirds of its body on the basking platform. Basking duration was recorded from the first photograph in which an individual was seen on the platform, to the first photograph in which it was absent. Thus, the minimum basking duration was 2 min (due to the 2 min time-lapse-photograph interval). To examine diel variation, treatments were categorized as 'night' (i.e. falling within a period of no light; 18:30–05:28 h) or 'day' (falling within a period of light; 05:30–15:58 h, based on the 'sunrise' [05:30 h] and 'sunset' [18:30 h] times for the room). Data recorded during the cleaning and maintenance period (16:00–18:30 h, described above) were excluded from analyses.

To describe body temperatures and thermal inertia of turtles, a biophysical model was constructed using an average-sized *E. m. krefftii* shell (220 mm; average carapace length of study population = 199.5 mm). A plastic bag filled with water was placed inside the shell to simulate a live turtle's body (model mass = 950 g; average mass of study population = 948.2 g), with two iButton temperature loggers placed inside the bag (Lutterschmidt & Reinert, 2012). This model was exposed to each temperature treatment sequentially, both in the water, and 'basking' for 2 h each (e.g. 2 h in cool water, followed by 2 h on the platform). For each treatment, the slope of a linear regression of temperature versus time was used to calculate the heating or cooling rate turtles would experience by moving from the water to basking and vice-versa.

Data analyses

All models were constructed via the package lme4 (v1.1.27.1; Bates et al., 2015), and significance was assessed using the ANOVA function in the car package (v3.0.12; Fox & Weisberg, 2019) with a type II sum of squares. Post hoc pairwise comparisons were made using a Tukey honest significant difference test. All analyses were conducted using R Statistical Software (v4.1.2; R Core Team, 2021).

A linear mixed effects model was used to test for effects of diel period (day or night), mass, and leech count (as fixed effects) on the median selected temperatures (response variable) of turtles during the thermal preference trials. Tank ID was included as an additional blocking variable (fixed effect), and turtle ID was included as a random effect.

For the basking trials, diurnal and nocturnal basking events were examined separately. This was because we wanted to test the effects of temperature on each type of basking (diurnal and nocturnal) rather than compare basking rates and durations between day and night. For each turtle, the total amount of time spent basking (i.e. the sum of the duration of all basking events per individual) was calculated for each temperature treatment. Not all turtles basked in every treatment; therefore, data were also classified into binary categories; 'basked' or 'did not bask' for each treatment. Binomial mixed effects models with each individual entered as a 1 ('basked') or a 0 ('did not bask') were used to test for effects of temperature (as a fixed effect) on the proportion of individuals that basked during the day or night, separately. A linear mixed effects model (day) and negative binomial mixed effects model (night) were used to examine the effects of temperature, mass, and leech count (as fixed effects) on the total amount of time spent basking. The biological variables (leech counts and mass) were included to account for variation in basking behaviour that may arise among individuals who differ in these factors. Body size is generally considered an important determinant of thermoregulatory behaviour among age/sex classes within reptiles (Bulté & Blouin-Demers, 2010b; Shine, 1980). Likewise, it has been suggested that leeches may influence basking behaviour in wild turtles via transmission of disease-causing haemoparisites (Ibáñez et al., 2015) and subsequent 'behavioural fever' which is induced to inhibit disease pathogenesis (Rakus et al., 2017 although, see Ryan & Lambert, 2005; Rossow et al., 2013). Leech and mass values were not included in all four models because we did not have sufficient data to include them without model convergence issues (see Table 2 for model terms used). For all models, turtle ID was included as a random effect, and the order of each temperature treatment was included as a fixed effect.

RESULTS

Preferred temperatures

The central 50% of selected temperatures, calculated per individual and averaged across individuals, ranged from 25.3°C (±SD: 1.5) to 27.6°C (±1.4) for diurnal trials and 25.3°C (±2.4) to 26.8°C (±2.5) for nocturnal trials (Figure 3a,b). Mean, median and modal selected temperatures were similar during night and day (Table 1).

There were no significant effects of diel period, mass, leech count or tank ID on variation in median selected temperatures (diel period [day or night]; $p=0.85$, mass; $p=0.73$, leech count; $p=0.23$, tank ID; $p=0.62$). The marginal model fit indicated that these terms accounted for only ~5% of the model variability ($R^2_{marginal}=0.05$). On the contrary, individual variation explained 64% the variation in selected temperatures ($R^2_{conditional}=0.64$).

Basking experiment

Thirty-one turtles were tested; however, three did not bask at any point, and so were removed from the analyses. An additional three turtles were removed because of malfunctions with the temperature control in the testing room. Thus, we had a sample size of 25 turtles (23 males and two females) that were run through three different temperature treatments. In one case, a basking event began at night and transitioned briefly into the day. This event was classed as 'night' because most of the basking event (>80%) occurred in darkness. Another individual basked continuously for 18 h and 47 min from 18:30 to 13:17 h. We split this event at 05:30 h (sunrise), classifying it as one nocturnal basking event (11 h), and one diurnal basking event (7 h and 47 min).

During the day, individuals were significantly more likely to bask when water temperatures were above the thermal preference (i.e. in the warm treatment), compared with at their preferred temperature (Figure 3c; Table 3). Meanwhile, proportions of individuals that basked diurnally in cool treatments were not significantly different from the other treatment groups (Table 3). Likewise, nocturnal basking events were more common, in terms of the proportion of individuals that basked at night, during warm treatments compared with preferred or cool treatments (Figure 3c), although this trend was not significant (Table 2).

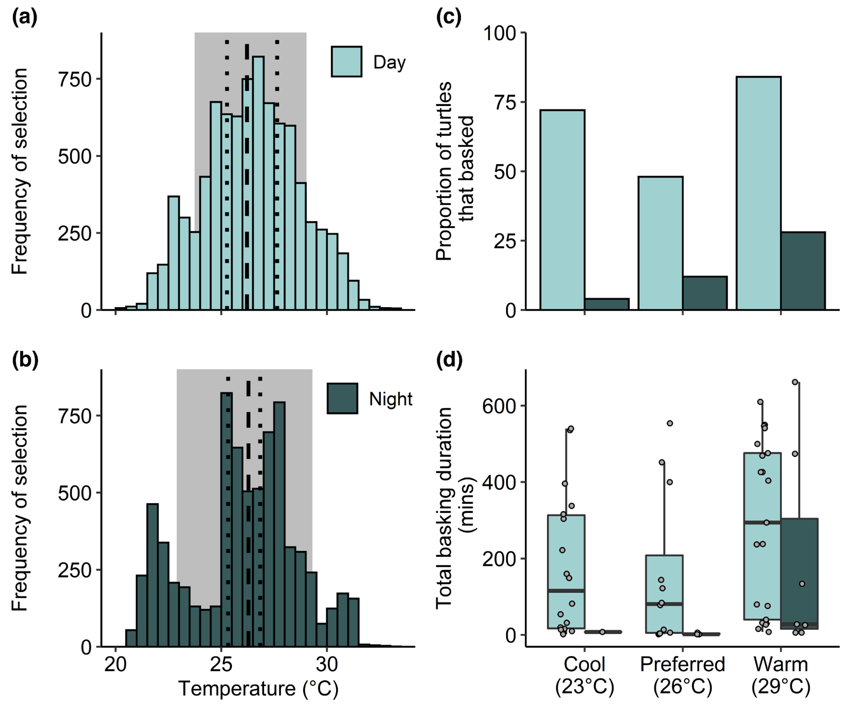

FIGURE 3 Selected temperatures of 22 male *Emydura macquarii krefftii* from the Ross River, Townsville, QLD, Australia, during diurnal (a) and nocturnal (b) periods. Dashed lines represent the median selected temperatures. Dotted lines represent the interquartile range (IQR; upper 75% and lower 25%) of selected temperatures. The margins of the grey boxes represent the lower IQR – the standard deviation of the lower IQR, and the upper IQR + the standard deviation of the upper IQR. Data include all selected temperatures (15 840 data points from 22 individuals). (c) The proportion of *E. m. krefftii* ($n = 25$) that basked at least once in a given treatment. (d) The total duration of all basking events for *E. m. krefftii* that basked at least once in a given treatment. Points overlaying box plots represent total basking durations for individual turtles. For total basking durations per treatment category that include data for turtles that did not bask, see Figure S2.

TABLE 1 Mean, median and modal temperatures (°C) for diurnal and nocturnal trial periods, calculated per individual, then averaged. The interquartile range (lower 25% and upper 75% of selected temperatures, that is Tset) is also displayed for day and night.

	Mean ± SD	Median ± SD	Mode ± SD	T_{set}	*N*
Day	26.51 ± 1.24	26.21 ± 1.51	26.15 ± 1.80	25.3°C ± 1.5–27.6°C ± 1.4	22
Night	26.12 ± 2.29	26.28 ± 2.42	26.00 ± 2.61	25.3°C ± 2.4–26.8°C ± 2.5	22

Turtles basked significantly longer in warm water treatments compared with other treatments, both day and night (Figure 3d; Table 3). The abundance of leeches on turtles had no significant influence on basking durations day or night, and mass had no significant influence on the duration of diurnal basking. We could not test the influence of mass on basking at night, as the nocturnal model would not converge with mass included due to low sample size (Table 2).

Biophysical model

The biophysical model gained heat at a linear rate of 0.0196°C/min when transferred from the 'cool' water treatment to the 'preferred' temperature on the basking platform, requiring 52 min to gain 1°C. The rate of heat loss, however, was curvilinear and decelerating. The model lost heat at

TABLE 2 Mixed effects model structures and results.

Test	Family	Fixed effects	Chi-sq	Df	*p*-Value
Diurnal: % of turtles basking	Binomial	Treatment temperature	7.18	2	0.03*
		Order of treatments	2.89	1	0.09
Nocturnal: % of turtles basking	Binomial	Treatment temperature	4.33	2	0.12
		Order of treatments	0.02	1	0.90
Diurnal: Total basking durations	Linear	Treatment temperature	19.11	2	<0.001*
		Order of treatments	11.17	1	<0.001*
		Leech counts	0.01	1	0.92
		Mass	0.56	1	0.45
Nocturnal: Total basking durations	Negative binomial	Treatment temperature	22.69	2	<0.001*
		Order of treatments	0.10	1	0.75
		Leech counts	0.76	1	0.39

Note: All models include turtle ID as a random effect.
*Statistically significant at $\alpha = 0.05$.

TABLE 3 Pairwise comparisons (*p*-values) for treatment groups ('warm', 'preferred' and 'cool') across each statistical model.

Test	Warm–Cool	Preferred–Cool	Warm–Preferred
% of diurnal basking	0.50	0.09	0.03*
% of nocturnal basking	0.11	0.51	0.31
Total diurnal basking durations	0.05*	0.15	<0.001*
Total nocturnal basking durations	<0.001*	0.71	<0.001*

Note: *p*-Values calculated using Tukey's Method.
*Statistically significant at $\alpha = 0.05$.

an overall rate of 0.0322°C/min when transferred from the 'warm' water treatment to the 'preferred' temperature on the basking platform, requiring 31 min to cool 1°C (Figure S3). The profile for heat loss was characterized by an initial rapid heat loss which gradually declined over the 2-h treatment. Overall, the model indicates that cooling initially occurs at nearly twice the rate of heating under the experimental conditions (i.e. turtles that leave warm water would lose heat at nearly twice the rate at which turtles that leave cool water would gain heat).

DISCUSSION

We found that tropical *E. m. krefftii* have relatively low preferred temperatures given the environment in which they live, and our results support the hypothesis that nocturnal basking is a mechanism for thermoregulatory cooling. Turtles in our trials preferred temperatures around 26°C. This is similar to observations of the active body temperatures of wild individuals of a related species (*Chelodina longicollis*: mean of 27.3°C, range of 23.7–32.2°C; Heatwole & Taylor, 1987). To our knowledge, this is the first study documenting the preferred temperatures of adult Australian tropical freshwater turtles using an aquatic thermal gradient. Macquarie river turtles (*Emydura macquarii macquarii*) thermoregulate in thermal gradients (Chessman, 2020), but preferred temperatures were not recorded in that study. Several studies have used aquatic thermal gradients to quantify thermal preferences for juvenile turtles from other countries: *Apalone spinifera*; 30–34°C (Feltz & Tamplin, 2007; Tamplin et al., 2020), *Mauremys reevesii;* 29–33°C (Xu et al., 2015), *Chelydra serpentina;* 27–33°C (Bury et al., 2000), *Trachemys scripta;* 30–33°C (Bury et al., 2000), *Pseudemys nelsoni;* 27–33°C (Nebeker & Bury, 2000), *Malaclemys terrapin*; 34°C (Tamplin et al., 2013) and *Glyptemys insculpta*; 30°C (Tamplin, 2006, 2009). Preferred temperatures measured in these studies were generally higher than those we observed for adult *E. m. krefftii*, but juveniles may favour elevated temperatures to promote development and growth (Tamplin et al., 2020). Heat-seeking behaviour is also characteristic of wild adult turtles in temperate climates, because environmental temperatures are lower than optimal ranges, especially in winter (Bulté & Blouin-Demers, 2010a, 2010b; Edwards & Blouin-Demers, 2007; Grayson & Dorcas, 2004; Millar et al., 2012).

Conversely, heat avoidance may be more important for *E. m. krefftii* if, as tropical ectotherms, they are heavily constrained by high temperatures (Deutsch et al., 2008; Huey et al., 2009, 2012; Tewksbury et al., 2008) or experience high risk of heat-related mortality (Vickers et al., 2011). In our study, the 'warm' treatment (29°C) turtles experienced in the laboratory was still cooler than aquatic temperatures they sometimes experience in their local habitat. In the Ross River, water temperatures frequently exceed preferred temperatures on summer nights (often surpassing 30°C), when the highest levels of nocturnal basking are observed (Nordberg and McKnight, 2023). Likewise, in the laboratory, *E. m. krefftii* actively avoided warm water during the day and night. Propensity to bask was greatly influenced by treatment temperatures, being more common and spanning longer periods in warm water treatments compared with other treatment groups. These results indicate a general aversion to high temperatures by tropical *E. m. krefftii* and suggest that nocturnal basking in the wild functions to lose heat. Meanwhile, turtles in this experiment tolerated low temperatures at night. Few individuals basked at night in cool or preferred treatments, and total nocturnal basking durations were similar for these treatments (mean durations = 8 and 3.33 min for cool and preferred treatments respectively; Table 3). Many individuals did, however, bask in cool treatments during the day, with turtles emerging for an average total duration of 177.5 min. There are two likely (and non-mutually exclusive) explanations for these patterns.

First, tropical reptiles are especially sensitive to warm temperatures. Tropical ectotherms are at risk of overheating because of high ambient temperatures (Deutsch et al., 2008; Huey et al., 2009, 2012) and because they experience substantial fitness declines when body temperatures surpass optimum levels (Huey et al., 2012; Martin & Huey, 2008). Thermal maxima can easily be exceeded in tropical reptiles' usual environment if thermoregulation is not perfect (Vickers et al., 2011). Therefore, thermoregulatory effort is expected to increase as environmental temperatures exceed preferred temperatures, and tropical reptiles should opt to maintain cautious, below-optimal, body temperatures as a 'safety net' for thermoregulatory imprecision (Martin & Huey, 2008; Vickers et al., 2011; Vickers & Schwarzkopf, 2016). Turtles in our trials basked more in warm treatments overall, possibly because of the increased fitness costs associated with being too warm. Alternatively, reduced basking activity in nocturnal cool treatments may have occurred because, under cool conditions, there was no need to provide a thermal safety margin. The need to avoid overheating may also explain why basking activity was similar between cool and preferred treatments overall, as the costs of choosing not to bask in these treatments are theoretically similar (i.e. no cost in preferred treatments and a low cost in cool treatments).

Second, basking at night when water temperatures are low and air temperatures are the preferred temperature is not an efficient strategy for gaining heat. Our biophysical model showed that, under nocturnal conditions, with no radiant heat, turtles on the basking platform would require 52 min to gain 1°C when emerging from 23°C water (the cool treatment) to 26°C (preferred air temperature). Conversely, they would require only 31 min to cool by 1°C when emerging from 29°C water (the warm treatment). In this study, *E. m. krefftii* invested very little time in basking at night when water temperatures were 'cool' or 'preferred'. Since nocturnal basking does not readily facilitate heat gain (Figure S3), and low body temperatures incur relatively low fitness costs in tropical reptiles (compared with being too warm; Martin & Huey, 2008), the best strategy to maximize thermal benefits may be to invest little-to-no effort in basking when the environment is already 'high quality' (i.e. at or slightly below preferred temperatures; Shine & Madsen, 1996; Vickers et al., 2011; Vickers & Schwarzkopf, 2016). Voluntarily maintaining lower body temperatures at night may also reflect the need to reduce metabolic costs when inactive (Clusella-Trullas & Chown, 2014).

In contrast to nocturnal basking patterns, approximately half the turtles basked during the day when both water and air temperatures were within the preferred temperature range (though diurnal basking rates were higher when the water was below or above preferred temperatures). In our experiment, diurnal basking was an ineffective mechanism for gaining heat, because turtles had no external source of radiation. It is possible that the experience of wild *E. m. krefftii* has led them to expect that light availability during the day represents opportunities for radiative heat gain. Thus, light may be an environmental cue that stimulates basking behaviour. In addition, basking may be influenced by factors beyond thermoregulation, explaining why some turtles chose to bask even when preferred temperatures could be attained by remaining in the water. Modulation of UV light exposure (photoregulation; Ferguson et al., 2003) could be an underappreciated function of diurnal basking, because it also facilitates homeostasis and is regulated via the same behaviours as thermoregulation (Conley & Lattanzio, 2022). Diurnal basking has also been proposed as a leech-removal mechanism (Mcauliffe, 1977), although a previous study found that basking (nocturnal and diurnal) is ineffective at removing leeches in *E. m. krefftii* (McKnight et al., 2021). Likewise, our study found no evidence that leech loads affect preferred temperatures or basking behaviour, though inferences are limited due to the lack of radiant heat. Further experiments using a UV light or a radiative heat source, or both, are required to determine how turtles would behave when exposed to these factors.

Conclusions

Preferred temperatures of *Emydura macquarii krefftii* ranged between 25.3 and 27.6°C during the day and 25.3 and 26.8°C at night. These ranges are both cool and narrow relative to average night-time water temperatures at the time of this study, implying the need for heat avoidance in the wild. In this study, *E. m. krefftii* basked more, in terms of both proportion of individuals and duration of emergence, when water temperatures were above-preferred temperatures compared with below them, demonstrating an avoidance of unfavourably warm water. This suggests that nocturnal basking is a mechanism for thermoregulatory cooling in this tropical system. Thermal preferences and thermoregulatory regimes of low-latitude turtles are poorly understood, so it would be instructive to observe the behaviour of wild individuals in relation to water temperature, to better understand their thermoregulatory choices under natural conditions.

AUTHOR CONTRIBUTIONS

Rosie Kidman: Conceptualization (supporting); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); project administration (equal); visualization (equal); writing – review and editing (lead). **Donald McKnight:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Lin Schwarzkopf:** Conceptualization (supporting); methodology (supporting); resources (equal); supervision (equal); writing – review and editing (equal). **Eric Nordberg:** Conceptualization (equal); data curation (supporting); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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