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How turtles keep their cool: Seasonal and diel basking patterns in a tropical turtle

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ABSTRACT

Behavioural thermoregulation by ectotherms is an important mechanism for maintaining body temperatures to optimise physiological performance. Experimental studies suggest that nocturnal basking by Krefft's river turtles (*Emydura macquarii krefftii*) in the tropics may allow them to avoid high water temperatures, however, this hypothesis has yet to be tested in the field. In this study, we examined the influence of environmental temperature on seasonal and diel patterns of basking in *E. m. krefftii* in tropical north Queensland, Australia. Wildlife cameras were used to document turtle basking events for seven consecutive days and nights for each month over a year (April 2020–March 2021). Air and water temperatures were recorded simultaneously using temperature loggers. We used a negative binomial mixed effects model to compare mean basking durations (min) occurring among four environmental temperature categories based on population thermal preference (26 °C): 1) air temperature above and water temperature below preferred temperature; 2) air temperature below and water temperature above preferred temperature; 3) air and water temperatures both above preferred temperature; and 4) air and water temperatures both below preferred temperature. Basking behaviour was influenced significantly by the relationship between air and water temperature. During the day, turtles spent significantly less time basking when both air and water temperatures were above their preferred temperatures. Conversely, at night, turtles spent significantly more time basking when water temperatures were warm and air temperatures were cool relative to their preferred temperature. This study adds to the growing body of work indicating pronounced heat avoidance as a thermoregulatory strategy among tropical reptile populations.

1. Introduction

Diurnal basking is a common thermoregulatory behaviour in reptiles (Cowles and Bogert 1944), including freshwater turtles (Boyer 1965; Schwarzkopf and Brooks 1985). Reptile basking is typically characterised by heliothermy, whereby exposure to solar radiation supplies the heat necessary for efficient development and physiological functioning (Parmenter 1980; Huey 1982; Carrière et al. 2008; Bulté and Blouin-Demers 2010a; Polo-Cavia et al. 2012). Heat gain can also be achieved *via* conduction to the animal through direct body contact with warm substrate or *via* convection from warm air. Patterns of thermoregulation are, therefore, closely tied to environmental conditions that facilitate body temperature optimisation (Boyer 1965; Obbard and Brooks 1979; Graham and Hutchison 1979; Ernst 1982; Crawford et al. 1983; Grayson and Dorcas 2004). Importantly, when the climate is warm or tropical, thermoregulation is also used to optimise body temperatures, rather than simply facilitating heat gain (Vickers et al. 2011).

Research on turtle basking has mostly been limited to patterns that occur during the day (e.g., Schwarzkopf and Brooks 1985; Bulté and Blouin-Demers 2010b, 2010a; Clavijo-Baquet and Magnone 2017) but recent studies have revealed that some turtles emerge from the water at night and engage in behaviour that, at least superficially, resembles diurnal basking (i.e., remaining alert but sedentary on exposed substrates for extended periods of time; Barhadiya et al. 2020; Kidman et al. 2023; McKnight et al. 2023; Nordberg and McKnight 2020, 2023). To date, this behaviour ("nocturnal basking") has been documented in seven families of freshwater turtle, but it appears to be restricted to tropical and subtropical populations, suggesting an influence of

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environmental temperatures (McKnight et al. 2023).

Aquatic habitats, unlike terrestrial ones, are characterised by a relatively high specific heat and conductivity, which can restrict the scope for behavioural thermoregulation by limiting independence of body temperatures from the water (Angilletta 2009; Seymour 1982). Further, the high heat capacity of water can produce nocturnal water temperatures that are higher than the air temperatures. The implication is that while nocturnal basking may not achieve thermoregulation by facilitating heat gain, due to a lack of solar radiation, it may allow tropical turtles to lose heat *via* evaporative cooling, conduction, or convection.

The association between nocturnal basking and environmental temperature is further supported by recent studies on Krefft's river turtles (*Emydura macquarii krefftii*) in tropical Australia. Turtles in this population frequently encounter nocturnal aquatic temperatures above their preferred thermal range (Kidman et al. 2023), and they regularly bask at night (McKnight et al. 2023; Nordberg and McKnight, 2020, 2023). In contrast, *E. macquarii* at cooler and more temperate sites further south (e.g., in Brisbane, Australia) bask at night less frequently (McKnight et al. 2023), and no nocturnal basking has been documented in *E. macquarii* south of Brisbane (e.g., Victoria and South Australia; Chessman, 1987; McKnight et al. 2023). In Townsville, where nocturnal basking is common, the behaviour often coincides with warm nights where water temperature is high (Nordberg and McKnight 2023), and an experimental laboratory study confirmed that *E. m. krefftii* basked more at night when the water temperature was above their preferred temperature range and the air temperature was within their preferred temperature range (26°C; Kidman et al. 2023).

To further investigate the relationship between temperature and basking patterns, we used camera traps to examine seasonal and diel patterns of both diurnal and nocturnal basking, and their relation to air and water temperatures in wild *E. m. krefftii*. We hypothesised that, if nocturnal basking is primarily driven by avoiding high water temperatures, nocturnal basking should increase in frequency, duration, or both when the water temperature is higher than the air temperature, and above this population's preferred temperature (26°C; Kidman et al. 2023). Further, we expected nocturnal basking to be more prevalent in the summer than in the winter. While diurnal basking is usually thought of as a mechanism for gaining heat, some studies have disagreed with that conclusion (e.g., Manning and Grigg 1997). Therefore, we also examined diurnal basking patterns with the prediction that, if diurnal basking primarily supports heat gain (as opposed to other functions such as UV regulation, parasite removal, or other non-thermoregulatory hypotheses; Ferguson et al. 2003; McKnight et al. 2021) then the highest levels of diurnal basking should occur in winter when water temperatures are low, and there should be reduced diurnal basking activity when the water is at or above the turtles' preferred temperatures. The present study builds on previous work on seasonal basking patterns in this population (Nordberg and McKnight 2023) by examining detailed seasonal and diel patterns, examining duration of basking events, and using the recently quantified preferred temperature (Kidman et al. 2023) to conduct explicit hypothesis testing.

2. Methods

2.1. Data collection and study site

This study was conducted on a population of *Emydura macquarii krefftii* in the Ross River in Townsville, tropical north Queensland, Australia. The basking site was a large, partially submerged branch (from a Paperbark *Melaleuca quinquenervia*) that extended from the riverbank across the surface of the water. It was approximately 6–8 m in length and 50–80 cm in diameter at its widest point and was dappled in sunlight through overhanging branches. The branch dipped into the water towards the end, allowing turtles to bask along its entirety.

We only used one basking site due to logistical constraints, however, this site was chosen because of its high level of basking activity (thus allowing us to obtain a large sample size of basking events). Additionally, the patterns of basking activity on this branch were representative of the larger area based on previous surveys (McKnight et al., 2023; Nordberg and McKnight 2023). A wildlife camera (CamPark T85™) was suspended at this common basking site and programmed to take a photo every 2 min with an infrared flash. The camera was suspended above the basking structure angled slightly downward (approx. 30°) to ensure the greatest amount of the basking structure could be observed in each photo (Fig. 1). The camera captured basking frequency, duration, and timing at the same location for seven consecutive days and nights of each month over a one-year period (date ranges = 22–29 Apr 2020; 12–19 May 2020; 22–29 Jun 2020; 23–30 Jul 2020; 14–21 Aug 2020; 22–29 Sep 2020; 13–20 Oct 2020; 10–17 Nov 2020; 23–30 Dec 2020; 24–31 Jan 2021; 13–20 Feb 2021; 10–17 Mar 2021). Due to a camera failure (low battery that led to the infrared flash not triggering at night), full day and night activity were only captured on two out of seven sampling nights during June. For all months, each photo was examined for basking turtles, with basking events defined as any period where a turtle emerged from the water with two-thirds or more of the body. The duration of an event spanned the time an individual spent on the basking substrate, from the first photo where it was present to the first photo in which it was absent, as conducted in previous studies (Kidman et al. 2023; McKnight et al. 2023). Thus, the minimum possible basking duration was 2 min. Although the number and position of turtles changed from photo to photo, we were able to keep track of individuals

Fig. 1. *Emydura macquarii krefftii* basking at our study site on a winter day (top; July 28, 2020, 13:58) and a summer night (bottom; January 31, 2021, 04:04). Images captured by wildlife cameras during the course of our study.

within a series of photos by carefully noting features such as body size, shell shape, scars, colouration, patterns of algal growth, and whether the turtle was wet (just emerged) or dry.

Turtles were not individually marked; therefore, some individuals may have contributed more than one basking event to the dataset. While potential pseudo-replication is a limitation of our study, we do not believe it seriously affected our results because the Ross River has a very high density of *E. m. krefftii* (Trembath 2005), and a large number of individuals used our basking log. We observed up to 15 turtles in a single photo, and a previous study surveying basking activity along this section of river documented up to 98 individuals basking simultaneously throughout the transect (Nordberg and McKnight 2023). Additionally, we frequently observed multiple turtles on the same log (including piled on top of each other), and we did not observe any antagonistic behaviours that would suggest that some individuals were monopolizing the log.

Environmental temperatures were measured using iButton temperature loggers (Thermochron TC DS 1921G) treated with a water-resistant coating (PlastiDip™; Roznik and Alford 2012). The iButtons recorded temperatures at 1-hr intervals in the air (attached to the basking log), near the water's surface (10 cm deep), at 1 m, and at 2 m depths over the same sampling periods as the wildlife camera deployments. Two additional, replicate iButton arrays were deployed at other basking logs in the study site. For each hour of each date, temperature measurements from all three replicate iButtons for each microhabitat were averaged across the three sites.

To convert the hourly temperature data (based on means from the three replicate arrays) into temperatures per basking event, an approximate temperature was calculated per minute (*via* regressions between each consecutive set of points [hours]), and those temperatures per minute were applied to each basking event and averaged. For example, if the following temperatures were recorded: 14:00 = 30 °C, 15:00 = 31 °C (a change of 0.0167 °C per minute), and a turtle basked for 4 min starting at 14:00, its mean basking temperature would be 30.025 °C (30 °C at 14:00, 30.017 °C at 14:01, 30.033 °C at 14:02, and 30.050 °C at 14:03). While this assumes a linear rate of temperature change, the change from 1 h to the next was generally small, and this should have provided a reasonable approximation of the temperature during a given basking event.

Basking events were categorized as having occurred during the night or during the day based on the average local sunrise and sunset times for each month. Thus, threshold times for day and night varied slightly among months to reflect actual seasonal changes in the diel cycle. To ensure that the dates and times of basking events aligned with the natural cycle of day and night, we started each 24-h period at sunrise to allow for a contiguous nocturnal period, rather than artificially splitting the nocturnal period into two dates at midnight. Observations of basking events that transitioned from day to night (n = 14) or *vice versa* (n = 83) were not included in the analyses.

Based on laboratory work, the preferred temperature (middle 50% of selected temperatures; T_{set}) of this population during the day is 25.3 °C (±SD: 1.5) to 27.6 °C (±1.4) and at night it is 25.3 °C (±2.4) to 26.8 °C (±2.5; Kidman et al. 2023). For both day and night, the mean, median, and mode of temperatures fell between 26.0 and 26.5 °C. Therefore, for the purposes of the current study, we used a single value (26 °C) as a cut off for both night and day to group environmental temperatures into the following four categories: 1) air temperature above and water temperature below preferred temperature; 2) air temperature below and water temperature above preferred temperature; 3) air and water temperatures both above preferred temperature; and 4) air and water temperatures both below preferred temperature. While this cut off point (26 °C) is useful logistically, it should be noted that some values slightly above and below 26 °C still technically fell within the turtles' preferred temperature range (defined as the interquartile range). Surface water temperature values (approx. 10 cm deep) were used for these calculations because this was the only water category for which we had robust data from all months (due to iButton failures and losses). The Ross River experiences little-to-no thermocline (we recorded a maximum depth of approx. 4 m in the middle of the river), especially over the summer months (Supplementary Fig. 1), so surface water temperatures should largely reflect deeper water temperatures.

2.2. Statistical analyses

For all analyses, basking duration and occurrence were examined for day and night separately. We used the cosinor test in the season package (v0.3.15; Barnett et al., 2022) to examine seasonal patterns in the number of basking events and mean duration of basking event per date. We assessed significance using the cosine result (Barnett and Dobson 2010). To compare mean durations of basking events among temperature categories, we used a negative binomial mixed effects model with temperature categories as a fixed effect and month as a random effect. Analyses were conducted using the package lme4 (v1.1.27.1; Bates et al. 2015) in R Statistical Software (v4.1.2; R Core Team 2021). Model significance was assessed using the Anova function in the car package (v3.0.12; Fox and Weisberg 2019) with a type II sum of squares, and *post hoc* pairwise comparisons were conducted *via* a Tukey HSD test.

We then compared the proportion of time that turtles spent basking in each temperature category (i.e., the sum of all minutes of basking in each category divided by the total minutes spent basking in any category) with the total proportion of time that occurred in each temperature category while the camera was deployed ("available"). We did this using a Monte Carlo simulation to account for the compositional nature of the data and the non-independence of sequential data points. First, we calculated the absolute values of the differences between the proportion of time spent in each category for basking turtles and available temperatures ("real absolute value"). Then, for each iteration, the simulation took each basking event and randomly selected a block of time of equal length and calculated the temperature per minute for that block (as described previously), resulting in a temperature for a "simulated basking event." Per iteration, we then calculated the absolute values of the differences between the proportion of time spent in each category for simulated basking turtles and available temperatures ("simulated absolute value"). This represented the expected result if turtles were basking randomly with respect to temperature categories. The simulation ran for 20,000 iterations and calculated simulated P values per temperature category by taking the number of iterations in which the real absolute value was greater than or equal to the simulated absolute value and dividing by the number of iterations (20,000). We created separate expected distributions for day and for night. Additionally, to provide a finer-scale assessment, the simulation was employed using each possible combination of air and surface water temperatures (at 1 min intervals) rather than the four temperature categories (e.g., time spent basking when water and air = 26 °C, when water = 26 °C and air = 27 °C; etc.). For all simulations, we used a slightly more conservative alpha of 0.01 to assess significance.

3. Results

We observed a total of 3220 diurnal basking events and 507 nocturnal basking events from April 2020–March 2021. Patterns of basking by *E. m. krefftii* varied strongly among seasons (Fig. 2). During the austral summer (November–February), daily basking patterns were unimodal with peaks in basking activity occurring in the early hours of the morning. In comparison, winter basking activity (June–September) followed a diurnal, bimodal distribution with peaks in the morning and afternoon. For example, in the middle of winter (July), the greatest basking activity occurred between 14:00–15:00, whereas in mid-summer (January), the greatest basking activity occurred between 03:00–04:00.

Total diurnal basking activity also followed a cyclical, seasonal pattern, with the most basking activity in the Austral winter (Fig. 2).

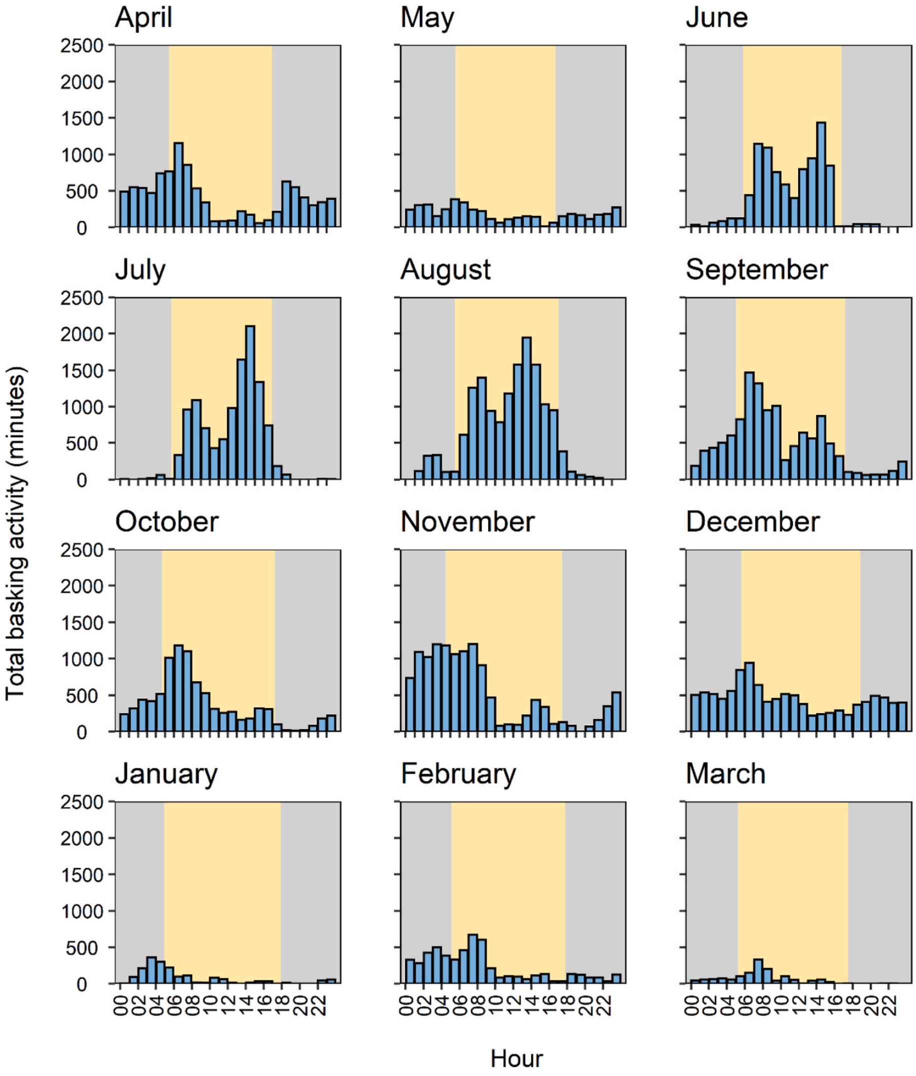


Fig. 2. Total *Emydura macquarii krefftii* basking activity (i.e., total amount of time turtles were observed basking) per hour per month (April 2020–March 2021). Day and night are indicated by yellow and grey shading, respectively. Due to camera malfunction, only two nights of data (but all seven days) were available for June.

Interestingly, based on the cosinor tests, this pattern was driven by changes in the average number of basing events per day ($t = -6.9$; $P < 0.001$) while the mean length of basking events remained largely stable ($t = 0.5$; $P = 0.627$; Fig. 3). Yearly nocturnal basking activity was also cyclical, but followed a reversed pattern, seldom occurring during the winter, gradually increasing as summer approached, peaking in early summer, and gradually declining (Fig. 2). In further contrast to diurnal patterns, seasonal changes in nocturnal basking patterns were driven by changes in the average length of basking events ($t = 3.4$; $P = 0.001$), not changes in the number of basking events ($t = -1.4$; $P = 0.158$).

During the day, there was no significant difference in mean durations of basking events among categories of environmental temperatures (i.e., the four categories defining the relationships between air temperature, water temperature and turtles' preferred temperature; negative binomial model: chisq = 0.420, $P = 0.936$; Supplementary Fig. 2; but see Monte Carlo results), however, mean nocturnal basking durations were affected by environmental temperature categories (chisq = 14.229, $P < 0.001$). Mean nocturnal basking durations were significantly shorter when both air and water temperatures were relatively cool (mean duration = 40 min) compared to when water temperatures were warm and air temperatures were cool (mean duration = 76 min; $P < 0.001$), relative to the turtles' preferred temperature. There was no significant difference in average nocturnal basking durations when both air and water temperatures were warm compared to other temperature categories (all other pairwise comparisons non-significant; all $P > 0.071$).

While there were no significant differences in the mean duration of diurnal basking events across months or temperature categories (Fig. 3), the Monte-Carlo simulations indicated that, during the day, turtles spent significantly less time basking than expected by chance when both air and water temperatures were above their preferred temperature (simulated $P < 0.001$); whereas they spent disproportionately more time basking when both air and water temperatures were below the preferred range (simulated $P < 0.001$) or when the air was below their preferred temperature and the water was above it (simulated $P = 0.001$; Figs. 4 and 5). At night, turtles spent significantly more time basking than expected by chance when the air was below their preferred temperature and the water was above it (simulated $P < 0.001$), and they spent significantly less time basking than expected by chance when the air and water were either both above (simulated $P = 0.002$) or both below their preferred temperature range (simulated $P < 0.001$; Figs. 4 and 5).

4. Discussion

We observed diurnal and nocturnal basking in all months of the year, but there was substantial variation among seasons, as well as associations with temperature. Our results largely matched our predictions and

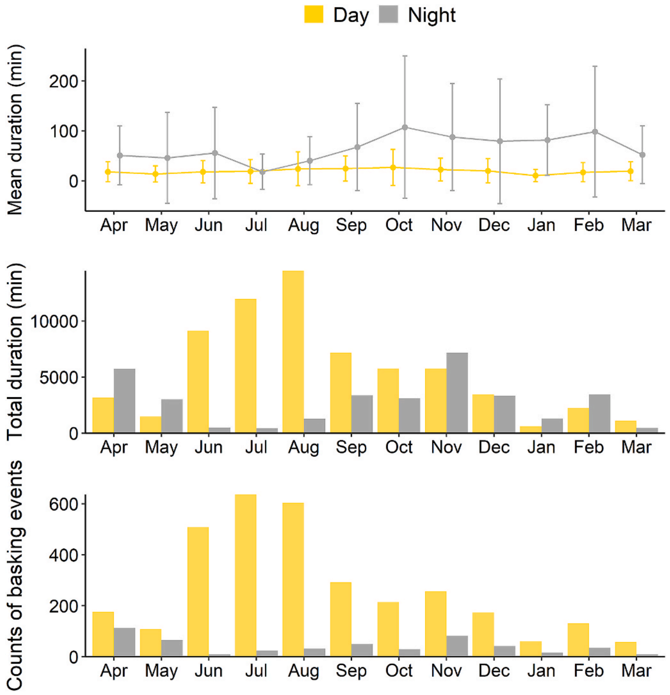
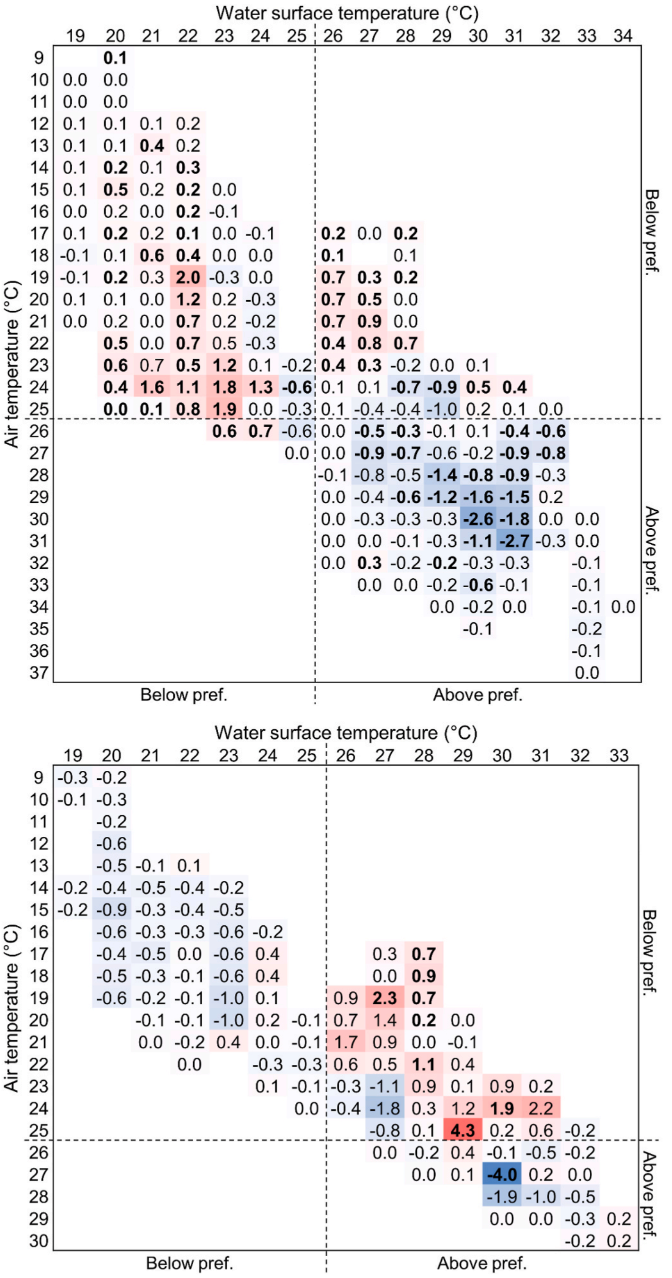


Fig. 3. Average duration of basking events (top panel), the total time turtles were observed basking (i.e., sum of all individual basking events; middle panel), and the number of individual basking events (as counts; bottom panel) for *Emydura macquarii krefftii* per month, split by day (yellow) and night (grey). Error bars represent the standard deviation of the mean duration of basking events. Due to camera malfunction, only two nights of data (but all seven days) were available for June.

suggest that diurnal basking is a thermoregulatory strategy to gain heat, while nocturnal basking is a thermoregulatory strategy to lose heat.

Diurnal basking events occurred far more frequently in the colder austral winter months (especially Jun–Aug), but the average duration of those events remained largely consistent across seasons (Fig. 3). This is consistent with the "shuttling" approach to thermoregulation used by many reptiles (Avery 1982; Huey 1982; Seebacher and Grigg 1997), wherein individuals periodically shuttle back and forth between warm and cool microenvironments, and cool conditions in winter required more frequent shuttling. We observed a seasonal shift in the timing of basking; from a unimodal summer distribution, with an early morning peak, to a bimodal winter distribution, with peaks in the morning and afternoon (Fig. 2). In both cases, there was reduced basking during the hottest part of the day. Likewise, our Monte-Carlo simulations showed that turtles were disproportionately less likely to bask diurnally when both air and water temperatures were above their preferred temperature (Fig. 4), choosing instead to bask diurnally when both air and water temperatures were low, and heat could be gained from solar radiation. Further, if water temperatures were elevated, diurnal basking was unlikely to occur even when air temperatures fell within the thermal preference range (Fig. 4), likely because the heat loss achieved by accessing relatively cool air temperatures was quickly negated by rapid radiative heat gains from exposure to sunlight. These findings support the conclusion that diurnal basking is at least largely a mechanism to facilitate heat gain.

Consistent with our predictions, patterns for nocturnal basking were more-or-less opposite to the diurnal patterns. In terms of both the mean duration of basking events and the total amount of time spent basking, nocturnal basking activity was highest in warmer months (Nordberg and McKnight 2023) and turtles spent a disproportionate amount of time basking at night when water temperatures were warm and air temperatures were cool, thus, allowing the turtles to cool. Further, they spent substantially less time basking nocturnally (i.e., shorter duration of basking events) when both water and air temperatures where above their thermal preference and basking would do little to facilitate heat loss. It is, additionally, worth noting that on average, nocturnal basking



Water surface temperature (°C)

Air temperature (°C)	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
9		**0.1**														
10	0.0	0.0														
11	0.0	0.0														
12	0.1	0.1	0.1	0.2												
13	0.1	0.1	**0.4**	0.2												
14	0.1	**0.2**	0.1	**0.3**												
15	0.1	**0.5**	0.2	**0.2**	0.0											
16	0.0	0.2	0.0	**0.2**	-0.1											
17	0.1	**0.2**	0.2	**0.1**	0.0	-0.1		**0.2**	0.0	**0.2**						
18	-0.1	0.1	**0.6**	**0.4**	0.0	0.0		**0.1**		0.1						
19	-0.1	**0.2**	0.3	**2.0**	-0.3	0.0		**0.7**	**0.3**	**0.2**						
20	0.1	0.1	0.0	**1.2**	0.2	-0.3		**0.7**	**0.5**	0.0						
21	0.0	0.2	0.0	**0.7**	0.2	-0.2		**0.7**	**0.9**	0.0						
22		**0.5**	0.0	**0.7**	0.5	-0.3		**0.4**	**0.8**	**0.7**						
23		**0.6**	0.7	**0.5**	**1.2**	0.1	-0.2	**0.4**	**0.3**	-0.2	0.0	0.1				
24		**0.4**	**1.6**	**1.1**	**1.8**	**1.3**	**-0.6**	0.1	0.1	**-0.7**	**-0.9**	**0.5**	**0.4**			
25		**0.0**	**0.1**	**0.8**	**1.9**	0.0	-0.3	0.1	-0.4	-0.4	-1.0	0.2	0.1	0.0		
26					**0.6**	**0.7**	-0.6	0.0	**-0.5**	**-0.3**	-0.1	0.1	**-0.4**	**-0.6**		
27							0.0	0.0	**-0.9**	**-0.7**	-0.6	-0.2	**-0.9**	**-0.8**		
28								-0.1	-0.8	-0.5	**-1.4**	**-0.8**	**-0.9**	-0.3		
29								0.0	-0.4	**-0.6**	**-1.2**	**-1.6**	**-1.5**	0.2		
30								0.0	-0.3	-0.3	-0.3	**-2.6**	**-1.8**	0.0	0.0	
31								0.0	0.0	-0.1	-0.3	**-1.1**	**-2.7**	-0.3	0.0	
32								0.0	**0.3**	-0.2	**-0.2**	-0.3	-0.3		-0.1	
33									0.0	0.0	-0.2	**-0.6**	-0.1		-0.1	
34											0.0	-0.2	0.0		-0.1	0.0
35												-0.1			-0.2	
36															-0.1	
37															0.0	

Water surface temperature (°C)

Air temperature (°C)	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
9	-0.3	-0.2													
10	-0.1	-0.3													
11		-0.2													
12		-0.6													
13		-0.5	-0.1	0.1											
14	-0.2	-0.4	-0.5	-0.4	-0.2										
15	-0.2	-0.9	-0.3	-0.4	-0.5										
16		-0.6	-0.3	-0.3	-0.6	-0.2									
17		-0.4	-0.5	0.0	-0.6	0.4			0.3	**0.7**					
18		-0.5	-0.3	-0.1	-0.6	0.4			0.0	**0.9**					
19		-0.6	-0.2	-0.1	-1.0	0.1		0.9	**2.3**	**0.7**					
20			-0.1	-0.1	-1.0	0.2	-0.1	0.7	1.4	**0.2**	0.0				
21			0.0	-0.2	0.4	0.0	-0.1	1.7	0.9	0.0	-0.1				
22				0.0		-0.3	-0.3	0.6	0.5	**1.1**	0.4				
23						0.1	-0.1	-0.3	-1.1	0.9	0.1	0.9	0.2		
24							0.0	-0.4	-1.8	0.3	1.2	**1.9**	2.2		
25									-0.8	0.1	**4.3**	0.2	0.6	-0.2	
26									0.0	-0.2	0.4	-0.1	-0.5	-0.2	
27										0.0	0.1	**-4.0**	0.2	0.0	
28												-1.9	-1.0	-0.5	
29												0.0	0.0	-0.3	0.2
30														-0.2	0.2

Fig. 4. Heat map displaying the difference between the proportion of time that turtles spent basking in each temperature category and the total amount of time available in each temperature category for the day (top panel) and the night (bottom panel). Negative, blue values indicate that turtles basked for less time than expected by chance, while positive, red values indicate that they basked for more time than expected by chance. Bold values indicate significant P values (at α = 0.01) based on 20,000 iterations of the Monte Carlo simulation. Results are shown in 1 °C intervals, but the data are grouped into the same four temperature categories used previously (top left; air and water below preferred temperature, top right; air below and water above preferred temperature, bottom left; air above and water blow preferred temperature, bottom right; air and water above preferred temperature). If nocturnal basking was a thermoregulatory strategy to escape hot water, then we expected disproportionately more nocturnal basking when the water was above their preferred temperature and the air was below their preferred temperature (top right).

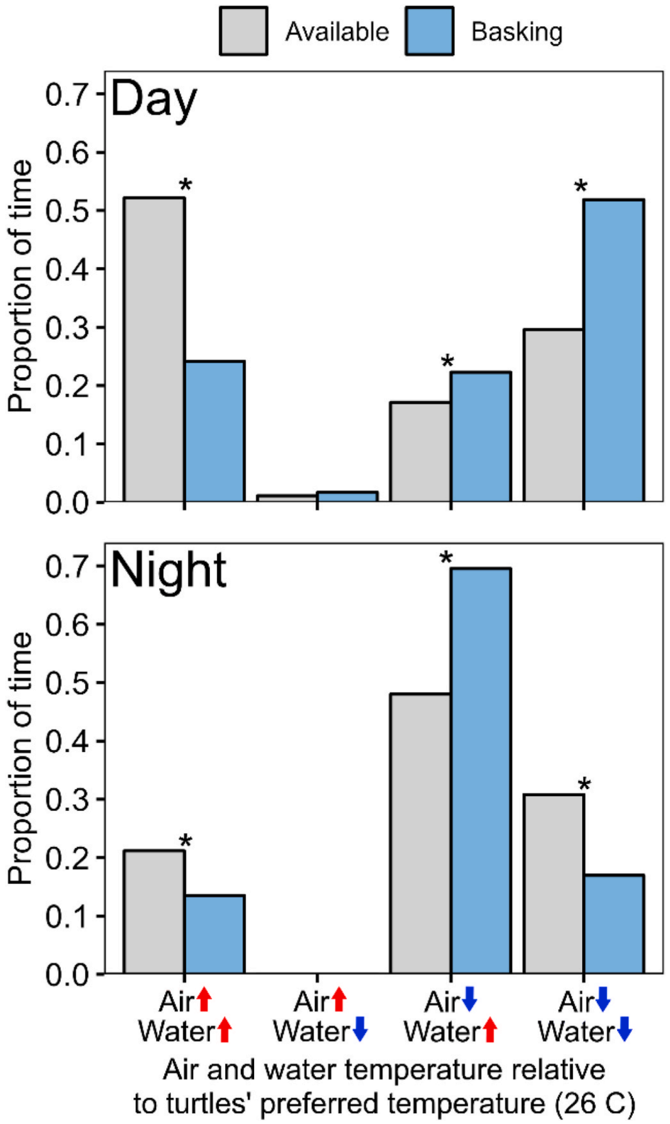


Fig. 5. The amount of time available in each temperature category (grey) compared to the amount of time turtles spent basking in each temperature category (light blue). Red, upward arrows indicate that the given environment (air or water) was above the turtles' preferred temperature (26 °C), and blue, downward arrows indicate that the environment was below the preferred temperature. * = statistically significant difference based on the Monte Carlo simulations.

events were considerably longer than diurnal basking events, which is consistent with rapid heat gain from the sun during the day compared to relatively slow heat loss from convection at night (Kidman et al. 2023).

These results are consistent with a previous field survey (Nordberg and McKnight 2023), a manipulative laboratory experiment (Kidman et al. 2023), and the broader observation that nocturnal basking in turtles is restricted to sub-tropical and tropical regions (Kidman et al. 2023; McKnight et al. 2023; Nordberg and McKnight 2023). It should also be noted that, as with previous studies (Nordberg and McKnight 2023), the turtles were alert and frequently moved their heads and limbs and changed positions. Thus, it does not appear that they were simply emerging to sleep. Taken together, these studies strongly suggest that, at least for this population, nocturnal basking is a thermoregulatory strategy to avoid overheating.

For tropical ectotherms, regulating body temperature frequently requires cooling, rather than heating, due to the high ambient temperatures of their environment (Kearney et al. 2009). Further, thermoregulation is not restricted to diurnal basking, with many nocturnal species engaging in temperature regulation in the absence of direct solar radiation (Kearney and Predavec 2000; Nordberg and Schwarzkopf 2019). In addition, typical reptile thermal performance curves show that fitness declines more rapidly for deviations above the thermal optimum than it does for shifts below the thermal optimum (Martin and Huey 2008). Thus, an important consideration for ectotherms is the high energetic costs and risk of mortality associated with exposure to elevated temperatures (Vickers et al. 2011; Vickers and Schwarzkopf 2016; Alford and Lutterschmidt 2018). It is therefore unsurprising that *E. m. krefftii* in this population are deterred from basking on hot days when doing so may result in elevated body temperatures. Likewise, it makes sense that on hot summer nights when the water temperature is above turtles' thermal preference, they bask in the relatively cool air to avoid unnecessarily high body temperatures. Indeed, environmental temperatures in this system frequently met these conditions during our study (Supplementary Fig. 3).

It should be noted that we use the term 'overheating' simply to indicate an increase in body temperatures beyond the thermal preference (26 °C) rather than to suggest that turtles in this system are reaching extreme or lethal temperatures. The physiological consequences of 'overheating' in this system, and the point at which they occur, are largely unknown. However, our observations here align with our experimental study (Kidman et al. 2023) which demonstrated that *E. m. krefftii* in the lab select cooler temperatures than would be easily accessible in the wild, suggesting the potential for significant physiological consequences of elevating body temperatures.

Changes in the timing of activity have also been documented in some North American freshwater turtles, in which nocturnal activity (as reflected by patterns in locomotion) is apparently driven by warm water temperatures (see Smith and Iverson 2004 for discussion). Such shifts in behavioural patterns coincident with geographic variation in the environment may allow evolutionary conservation of thermal physiology among populations (e.g., Weatherhead et al. 2012; Muñoz and Losos 2018). Within populations, shifts in diel activity period may occur from day to night, or *vice versa*, depending on thermal conditions. For example, Arenas-Moreno et al. (2018) demonstrated that several nocturnal tropical skinks are diurnal when high thermal quality environments are available during the day. Likewise, Weatherhead et al. (2012) and Sperry et al. (2013) demonstrated activity shifts from day to night in a terrestrial snake (*Elaphe obsoleta*) in response to high day-time temperatures. A similar behaviour was also documented in an Australian tropical snake (*Tropidonophis mairii*; Abom et al. 2012) that switches from diurnal to cathemeral depending on seasonal temperatures. Such switches in daily and seasonal activity patterns are an important mechanism of behavioural thermoregulation in ectotherms (Stevenson 1985; Porter et al. 1973). Given the high ambient temperatures characteristic of north-eastern Australia, it is unsurprising that *E. m. krefftii* are frequently exposed to temperatures above their thermal optimum. It is likely that this population may preferentially adjust their diel activity patterns to exploit higher-quality thermal opportunities when available.

Shifts to nocturnal activity may facilitate thermoregulation by buffering high diurnal temperatures (e.g., DeGregorio et al. 2015; Levy et al. 2019). Such flexibility may be an important mitigator of climate vulnerability, especially as adaptation to warmer temperatures is considered 'feasible but unlikely' due to the limited acclimation ability of tropical reptiles (Huey et al. 2009). An important aspect of this limitation is that upper thermal tolerances (critical thermal maximum; CT_{max}) in ectotherms are more constrained than lower tolerances (critical thermal minimum; CT_{min}; see Clusella-Trullas and Chown 2014 for discussion) which places a biological restriction on adaptation to climate change. In the future, the capacity for tropical reptiles to cool by thermoregulating may be crucial to maintaining fitness (Tewksbury et al. 2008; Huey et al. 2009). However, given that night-time temperatures are increasing faster than day-time temperatures under climate change (Davy et al. 2017; Gaston 2019), shifting activity periods may only go so far to allow reptiles to remain within preferred temperature ranges in warming environments. Crucially, even small increases in temperature can translate into extreme climate conditions in tropical and subtropical regions (Beaumont et al. 2011), and freshwater turtles are already impacted by several environmental and human factors that are likely to be exacerbated by warming climates (Stanford et al. 2020; Bower et al. 2023; Petrov et al. 2023).

Turtles in this population actively thermoregulate during the day and night, but more work is needed to understand how resilient to climate change these behaviours make them, and, more generally, what capacity tropical and sub-tropical reptiles have for adapting to climate change. One limitation of this study is that, while we were able to describe broad-scale patterns in basking behaviour at the population level, the fine-scale dynamics of body temperature variation of individual turtles is lacking. Ascertaining these body temperatures, either through trapping and tagging or using biophysical models, would be a valuable next step in further understanding the behaviour of this population.

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CRediT authorship contribution statement

Rosie Kidman: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Donald T. McKnight:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Lin Schwarzkopf:** Project administration, Supervision, Writing – review & editing. **Eric J. Nordberg:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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