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RESEARCH ARTICLE

Seasonal, environmental and anthropogenic influences on nocturnal basking in turtles and crocodiles from North-Eastern Australia

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Abstract

Many ectotherms bask in the sun as a behavioural mechanism to increase body temperature and facilitate metabolism, digestion or gamete production, among other functions. Such behaviours are common during the day, but some nocturnal species are also known to thermoregulate at night, in the absence of solar radiation, through shifts in body posture or microhabitat selection. Additionally, recent work has documented nocturnal basking in freshwater turtles in tropical Australia, though the purpose of the behaviour remains unknown. Here, we have built upon that work to test: 1. seasonal differences, 2. the influence of environmental factors and 3. the influence of anthropogenic development (e.g. riverfront houses) on nocturnal basking behaviour. We visually surveyed transects repeatedly at night on the Ross River, Townsville, QLD, Australia from March to November 2020 and documented nocturnal basking in both freshwater turtles (*Emydura macquarii krefftii*) and freshwater crocodiles (*Crocodylus johnstoni*). For both taxa, we found significantly more nocturnal basking activity during the hotter months. Likewise, water surface temperature significantly influenced nocturnal basking in both taxa, especially when water temperatures were both high and warmer than air temperatures. We propose that nocturnal basking provides a mechanism for thermoregulatory cooling when water temperatures are high (e.g. 30°C) and above-preferred temperatures. After accounting for availability in basking habitat, both turtles and crocodiles basked more frequently on the undeveloped side of the river, suggesting avoidance of human activity or disturbance. This study is the first to document nocturnal basking activity temporally throughout the year as well as the first to identify the influences of environmental factors. Nocturnal thermoregulation has been documented in many reptiles, however, thermoregulatory cooling in tropical systems is less well-known.

KEYWORDS
ectotherm, moon phase, reptile, thermoregulation, thermoregulatory cooling, tropics

INTRODUCTION

Most reptiles cannot maintain their body temperature physiologically and must rely on external sources of heat (Cowles & Bogert, 1944; Huey, 1982). This limitation does not, however, place them entirely at the mercy of the environment's vagaries. Reptiles are adept at maintaining preferred body temperatures through behavioural thermoregulation by using both microenvironments and body postures to their advantage in both aquatic and terrestrial environments (Doody et al., 2002; Hertz et al., 1993; Huey et al., 1989). Remaining in the sun ('basking' or 'sunning') is one such behaviour that is common throughout Reptilia (Heatwole & Taylor, 1987) and is particularly conspicuous in crocodilians and many freshwater turtles, which are frequently seen exposed on logs and rocks that protrude from the water (Boyer, 1965; Modha, 1968). The primary purpose of basking is contested in the literature, described below, and is likely useful for multiple, non-exclusive reasons.

Curiously, some crocodilians and freshwater turtles will engage in a similar behaviour at night, which has been termed 'nocturnal basking' (Nordberg & McKnight, 2020), where animals emerge from the water and bask on emergent logs along waterways. This behaviour is well documented in crocodilians (Cott, 1961; Modha, 1968; Vyas, 2018) but has only recently been documented in aquatic turtles (Barhadiya et al., 2020; Cann & Sadlier, 2017; Nordberg & McKnight, 2020). The purpose and significance of this behaviour at night remain elusive. One possibility is that animals are simply resting, and it has been anecdotally reported that crocodiles emerge from the water more frequently on rough nights with high winds (Cott, 1961; Thorbjarnarson, 1989). However, both crocodiles and turtles frequently bask at night in calm conditions and around water with little or no flow (Barhadiya et al., 2020; Nordberg & McKnight, 2020). Removal of ectoparasites, algae and fungi through the drying of the skin and scutes has also been postulated as a potential reason for diurnal basking (Boyer, 1965; Cagle, 1950; Neil & Allen, 1954), but there is little evidence to support this hypothesis. A recent experimental study found that basking was ineffective at removing leeches on turtles unless basking continued for much longer periods than typical for the population being studied (McKnight et al., 2021). Predator avoidance has also been suggested (Barhadiya et al., 2020; Nordberg & McKnight, 2020), but this hypothesis has yet to be tested, possibly due to logistical constraints in removing or controlling for predators in natural or artificial systems. Finally, nocturnal basking may be thermoregulatory. Thermoregulation may be especially important in tropical systems, where aquatic reptiles may emerge at night to cool down if the water is too warm (Nordberg & McKnight, 2020; Thorbjarnarson, 1989). Indeed, mouth gaping, a behaviour that is generally thought to be primarily thermoregulatory (Heatwole et al., 1973), but may also have additional functions, has been observed in several crocodilians at night (Carl et al., 2020; Loveridge, 1984; Price et al., 2022).

Relatively, little attention has been paid to the potential purpose of nocturnal thermoregulation in reptiles. However, some studies have found that reptiles can regulate their nocturnal body temperatures through microhabitat selection (Amadi et al., 2020; Kearney & Predavec, 2000; Nordberg & Schwarzkopf, 2019). Previous work has generally focussed on terrestrial environments, but the high thermal capacity of water may evoke different behaviours in aquatic reptiles, such as emerging at night to cool down, especially in tropical systems.

To begin examining this possibility, we expanded on our previous work documenting nocturnal basking in Krefft's river turtles (*Emydura macquarii krefftii*) in Townsville, Australia (Nordberg & McKnight, 2020). Here, we used a standardized protocol to conduct repeated surveys throughout the year to test for seasonal differences in nocturnal basking behaviour in turtles and crocodiles. We also tested if environmental (e.g. water temperature, wind speed, moon phase) or anthropogenic factors influenced basking frequency.

METHODS

Study site and species

The Ross River is a major watercourse running from the Ross River Dam, south of Townsville in tropical north Queensland, Australia and winds through the city centre before emptying into the Coral Sea. From the dam to the river mouth, the Ross River is approximately 30 km long and 150 m wide at parts (between 50 and 100 m wide at the study site). Flow volume and river height in the Ross River are regulated by the Ross River Dam and were fairly consistent throughout the duration of this study. The river supports a variety of wildlife, including populations of Krefft's river turtles (*Emydura macquarii krefftii*) and freshwater crocodiles (*Crocodylus johnstoni*). The first 10 km of the river, as it leaves the Ross River Dam, is bordered by open *Eucalyptus* bushland with no development on the eastern bank and river-front residential housing and public parks on the western bank (Figure 1). Some recreational boating and swimming occur throughout the length of the river, however, none of these activities were observed at night when the transects were surveyed. The Ross River was selected as the study site due to the abundance of *E. m. krefftii* and *C. johnstoni*, access to the river, and because nocturnal basking had been previously described from this location (Nordberg & McKnight, 2020).

Available basking habitat

Prior to conducting basking surveys, we assessed the riverbanks along a 4 km transect approx. 20 km upstream from the mouth of the river (including both sides of the riverbanks; thus 8 km of river bank) by counting potential basking structures (e.g. overhanging and emerging branches, rocks, logs) that could be used for aerial basking. Basking structures were not identified for turtles or crocodiles separately but were included if they were large enough in diameter (e.g. >20 cm) to support either animal of varying sizes. We quantified basking structure availability to identify if particular sections along the transect may be biased in their potential to support basking individuals. On both sides of the river, the land sloped to the water, where it was possible for animals to bask on the bank itself throughout the entirety of the study area. Because the banks were available throughout the entire area, they were not included as potential basking structures in the analyses. The river height remained relatively stable throughout the duration of the study and all emergent basking structures remained accessible.

Basking surveys

We conducted repeated nocturnal riverbank surveys from March to November 2020 along the Ross River ($n = 31$ surveys total). During each survey, one person (EN) used a canoe with an attached electric propeller (Watersnake ASP T24-SW Electric Motor) to cruise along each bank of the transect (a total of 8 km of riverbank per survey). Each transect was completed in ~2 h (20:00–22:00). Turtles and crocodiles were identified basking at night using a headtorch (Ledlenser H14.r) from the canoe travelling at a constant rate of 2 km per hour. Crocodiles were also easily identifiable from their distinctive eyeshine from a headtorch even while in the water. The location of each animal was recorded (either in the water or out of the water). We use the term 'nocturnal basking' to describe an animal out of the water,

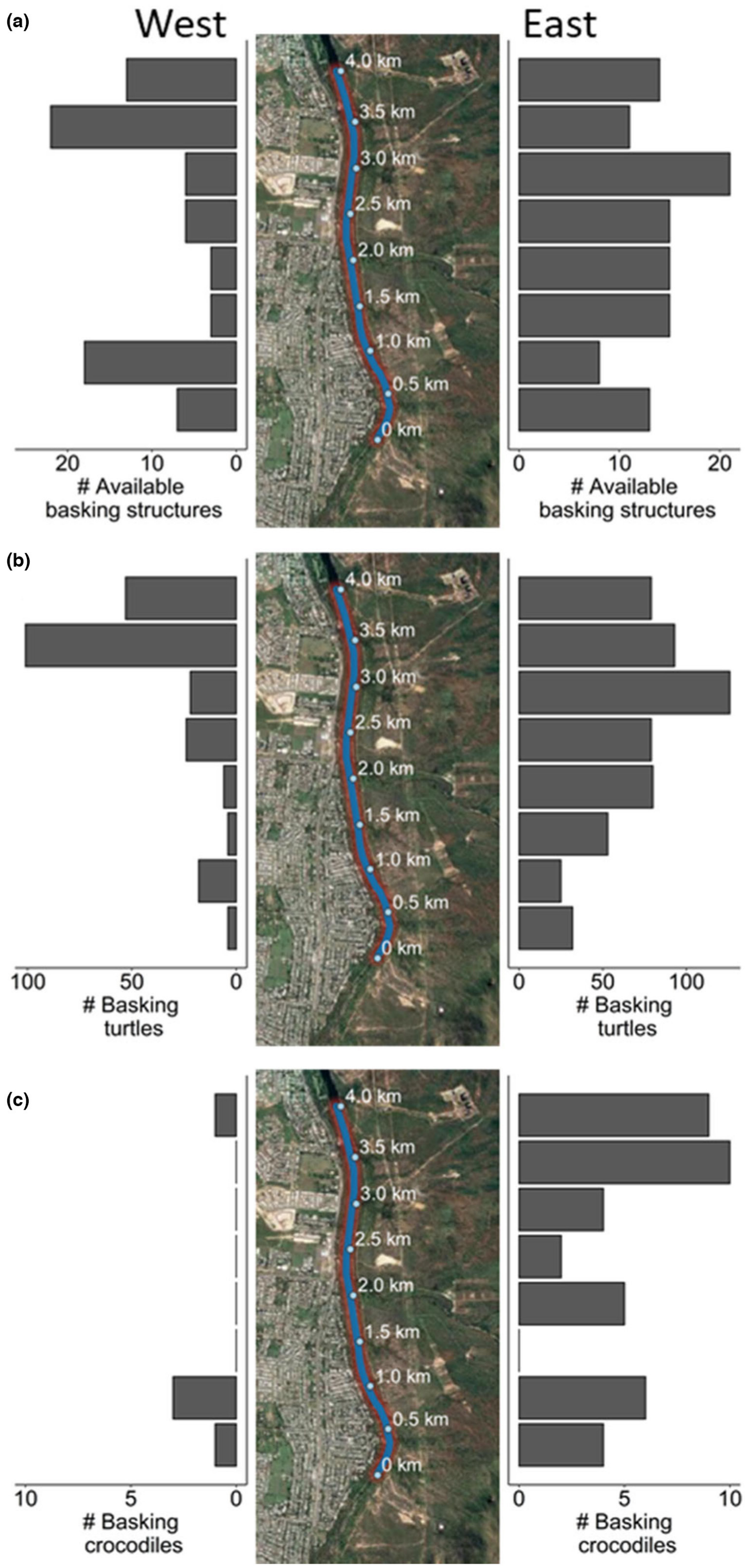

FIGURE 1 The study site, a 4 km stretch of the Ross River was surveyed from March to November 2020 via canoe. Both the east and west sides of the riverbank were searched for nocturnal basking activity in Krefft's river turtles (*Emydura macquarii krefftii*) and freshwater crocodiles (*Crocodylus johnstoni*). The 0.5 km sections used in the basking structure analysis are shown (i.e. each bar shows a transect section for the west or east bank).

perched on a log, rock or on the riverbank at night. The size of individuals was estimated as follows: turtles = 'large' (mature adults; straight carapace length > 15 cm) or 'small' (juveniles; straight carapace length < 15 cm), crocodiles = large (>2 m in total length), medium (between 1–2 m in total length) or small (<1 m in total length).

Weather conditions (e.g. air temperature, water surface temperature, humidity, average wind speed [2 min average]) were recorded at the beginning of each survey with a handheld Kestrel unit (Kestrel 3000, Kestrel Australia, Victoria, Australia) and a handheld digital thermometer probe (Table 1). Moon illumination data (% full) were acquired for the survey date and time from www.timeanddate.com.

Data analyses

Seasonality in nocturnal basking frequency

We used circular statistics from the cosinor test in the *season* package (v0.3.15; Barnett et al., 2022) to test for seasonal changes in nocturnal basking frequency for both freshwater turtles (*E. m. krefftii*) and crocodiles (*C. johnstoni*). Following the recommendations of Barnett and Dobson (2010), we assessed the significance using the cosine result.

Basking habitat selection

We used generalized linear mixed effects models to test whether the availability of basking structures influenced nocturnal basking frequency and whether anthropogenic factors (houses and human activity) affected nocturnal basking frequency after controlling for differences in structure availability. We created two separate models, one for turtles and one for crocodiles. For each model, we split the river into eight 0.5 km sections and used the total number of nocturnal basking events per section per riverbank side (east or west) summed across all surveys as the response variable. The number of available basking structures per segment per river bank side and the river bank side were included as fixed effects and the transect segment was included as a random intercept. The model for turtles used a negative binomial distribution while our

TABLE 1 Environmental data were collected at the beginning of each survey along the Ross River, Townsville, QLD, Australia.

Environmental variables	Description
Air temperature	Air temperature (°C) was recorded with a Kestrel 3000 weather unit at the beginning of each survey within 5 m of the bank.
Water surface temperature	Water surface temperature was measured within 5 m of the bank using a handheld digital thermometer, placing the probe into the water approx. 5–10 cm under the water.
Humidity	Humidity (%) was measured with a Kestrel 3000 immediately after air temperature.
Average wind speed	Average wind speed was measured (kpm) with a Kestrel 3000 over 2 min at the beginning of each survey.
Moon illumination	Moon illumination (% full) was taken from www.timeanddate.com for the location of Townsville, QLD, Australia.

model for nocturnally basking crocodiles used a zero-inflated Poisson distribution due to the high number of zeros.

Influence of environmental conditions

We checked for multicollinearity among our environmental variables and removed a variable if it was highly correlated with another (e.g. air temperature and water surface temperature were highly correlated, so we only used water temperature in our models). To identify whether nocturnal basking frequency was influenced by environmental conditions, we fit generalized linear models (GLM; Bates et al., 2015) using nocturnal basking frequency (number of individuals basking per survey) as a response variable and water surface temperature, wind speed, humidity and moon illumination (% full) as fixed effects. We conducted model selection using the dredge function in the package *MuMIn* (v1.43.17; Barton, 2020) based on Akaike's information criterion (AICc, corrected for small sample sizes). Models with the lowest AICc values had the greatest explanatory power, model fit and model parsimony (Burnham & Anderson, 2004). Model averaging was used when no optimal model could be identified (i.e. there were multiple top models with ΔAICc <2; Mazerolle, 2020). Final models were validated by examining deviance residual plots. Further, we calculated model fit values with pseudo-R^2 values for each model (Nakagawa & Schielzeth, 2013).

RESULTS

Freshwater crocodiles (*C. johnstoni*) were reliably identified and counted by eyeshine in all sections of the river, regardless of whether they were basking or not. We observed 21.6 ± 3.33 crocodiles per survey (mean ± SD; including animals observed in the water), resulting in high densities of freshwater crocodiles: 5.4 crocodiles per 1 km of river. Turtles were rarely observed swimming in the water during our nocturnal surveys but were often observed basking at night (39.7 ± 35.6 turtles per survey, 9.9 turtles per 1 km of river).

Size class

Adult and juvenile turtles were observed basking at night. However, it was more common to see adult turtles (Table 2). Conversely, we observed a wide range of crocodile sizes basking at night, including small, medium and large individuals (Table 2).

Habitat selection

Basking turtles used emergent logs exclusively when basking at night, while crocodiles basked on both emergent logs and on the riverbank (Figure 2). Our mixed effect models indicated more basking structures (predominantly logs) were available on the eastern side of the river (bordered by bushland) than on the western side (largely bordered by residential properties), but even after accounting for that difference in availability, both turtles and crocodiles basked more often on the eastern side of the river (turtles: $\chi^2 = 32.009$, df = 1, $p < 0.001$; crocodiles: $\chi^2 = 18.467$, df = 1, $p < 0.001$; Figure 1).

TABLE 2 Size distribution of nocturnally basking freshwater Krefft's river turtle (*Emydura macquarii krefftii*) and freshwater crocodiles (*Crocodylus johnstoni*). Mean monthly frequencies per survey are displayed with proportions per survey in parentheses. Turtle sizes were estimated visually as 'large' (mature adults; straight carapace length > 15 cm) or 'small' (juveniles; straight carapace length < 15 cm). Crocodile sizes were characterized as large (>2 m in total length), medium (between 1 and 2 m in total length) or small (<1 m in total length).

		Krefft's river turtle (*Emydura macquarii krefftii*)		Freshwater crocodile (*Crocodylus johnstoni*)		
Month	**Surveys (n)**	**Large**	**Small**	**Large**	**Medium**	**Small**
Mar	1	53.0 (0.93)	4.0 (0.07)	1.0 (0.50)	1.0 (0.50)	0.0 (0.00)
Apr	3	74.0 (0.90)	8.0 (0.10)	1.7 (0.36)	2.7 (0.57)	0.3 (0.07)
May	4	20.5 (0.99)	0.25 (0.01)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Jun	2	3.5 (1.00)	0.0 (0.00)	0.0 (0.00)	0.5 (1.00)	0.0 (0.00)
Jul	3	2.3 (0.88)	0.3 (0.13)	0.3 (0.50)	0.0 (0.00)	0.3 (0.50)
Aug	3	2.3 (1.00)	0.0 (0.00)	0.7 (0.67)	0.3 (0.33)	0.0 (0.00)
Sep	5	26.6 (0.94)	1.6 (0.06)	0.0 (0.00)	0.6 (0.75)	0.2 (0.25)
Oct	4	64.5 (0.97)	1.8 (0.03)	0.8 (0.60)	0.0 (0.00)	0.5 (0.40)
Nov	5	81.4 (0.97)	2.2 (0.03)	1.6 (0.57)	1.2 (0.43)	0.0 (0.00)

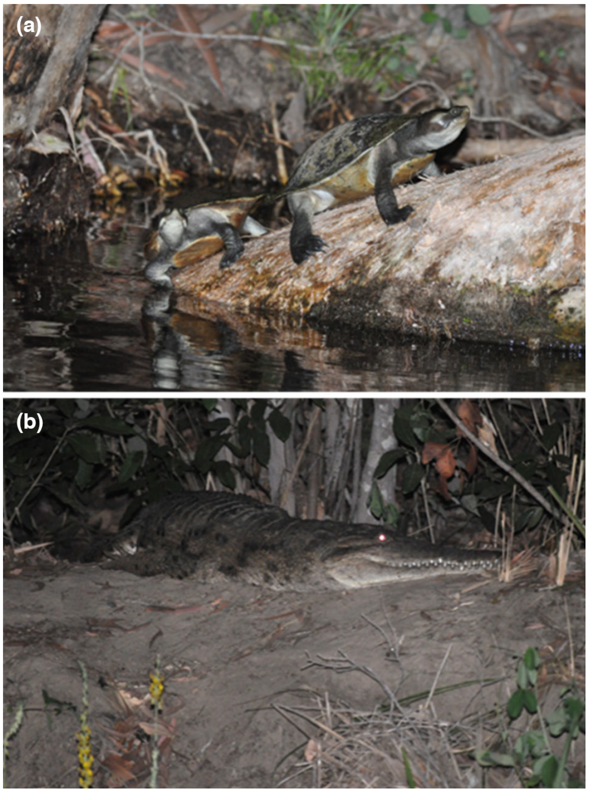

FIGURE 2 Two adult Krefft's river turtles (*Emydura macquarii krefftii*; a) and a large freshwater crocodile (*Crocodylus johnstoni*; b) basking along the riverbank in the Ross River, Townsville, QLD, Australia. Photos by E. Nordberg.

Seasonal patterns and environmental factors

There were significant seasonal patterns for nocturnally basking turtles ($t = 10.193$, $P < 0.001$) and nocturnally basking crocodiles ($t = 3.189$, $p = 0.004$; Figure 3), but not for overall nocturnal crocodile sightings ($t = 0.486$, $p = 0.631$), which is to be expected given their visibility via eye-shine even when in the water. Turtles were observed basking at night in

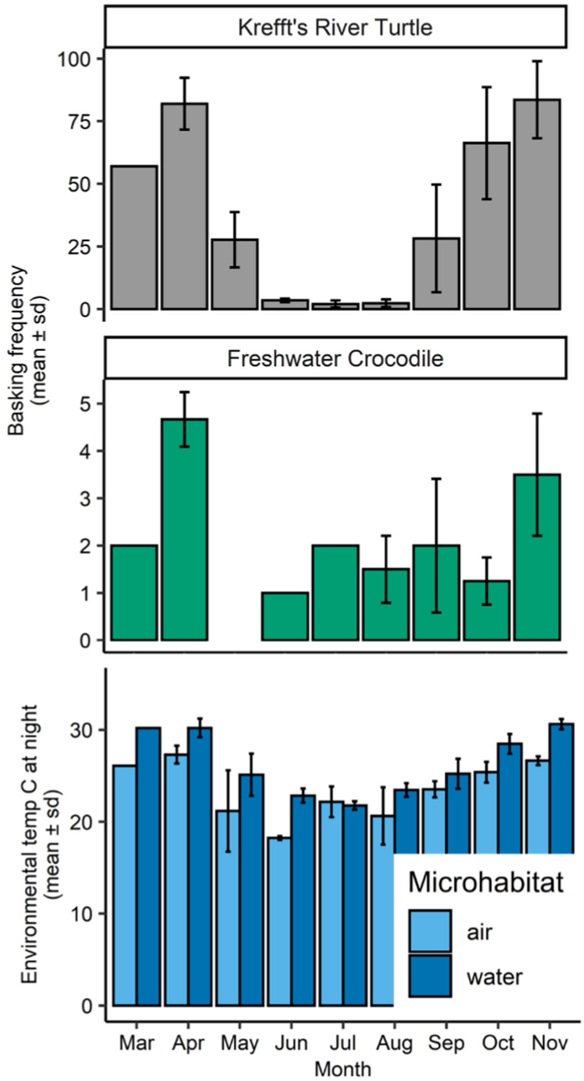

FIGURE 3 Seasonal patterns of nocturnal basking activity in freshwater turtles (*Emydura macquarii krefftii*; top [grey]) and freshwater crocodiles (*Crocodylus johnstoni*; middle [green]). Bars show the mean number of individuals per survey and error bars show one standard deviation (1–5 surveys were conducted per month). Both species showed strong seasonal effects, with higher occurrences of nocturnal basking in the summer months with high environmental temperatures (bottom [blue]).

every month of our study (March–November), while crocodiles were observed basking at night in every month except May (Figure 3). Significantly fewer turtles and crocodiles emerged at night to bask during the winter when air and water temperatures were lowest (Figure 4). Model selection on our generalized linear models (Table 3) indicated that water surface temperature and average wind speed were important variables to be included in predicting the frequency of nocturnally basking freshwater turtles. However, only water surface temperature showed a significant effect on the number of basking turtles ($\chi^2 = 169.409$, $p < 0.001$; Table 4). Similarly, for freshwater crocodiles, water surface temperature, humidity, and moon illumination were important factors in the model. However, only water surface temperature showed a significant influence on nocturnal basking ($\chi^2 = 4.239$, $p < 0.001$; Table 4).

Some surveys ($n = 16/31$) were conducted on nights with no wind. As a result, any effects of wind could have been masked by variations

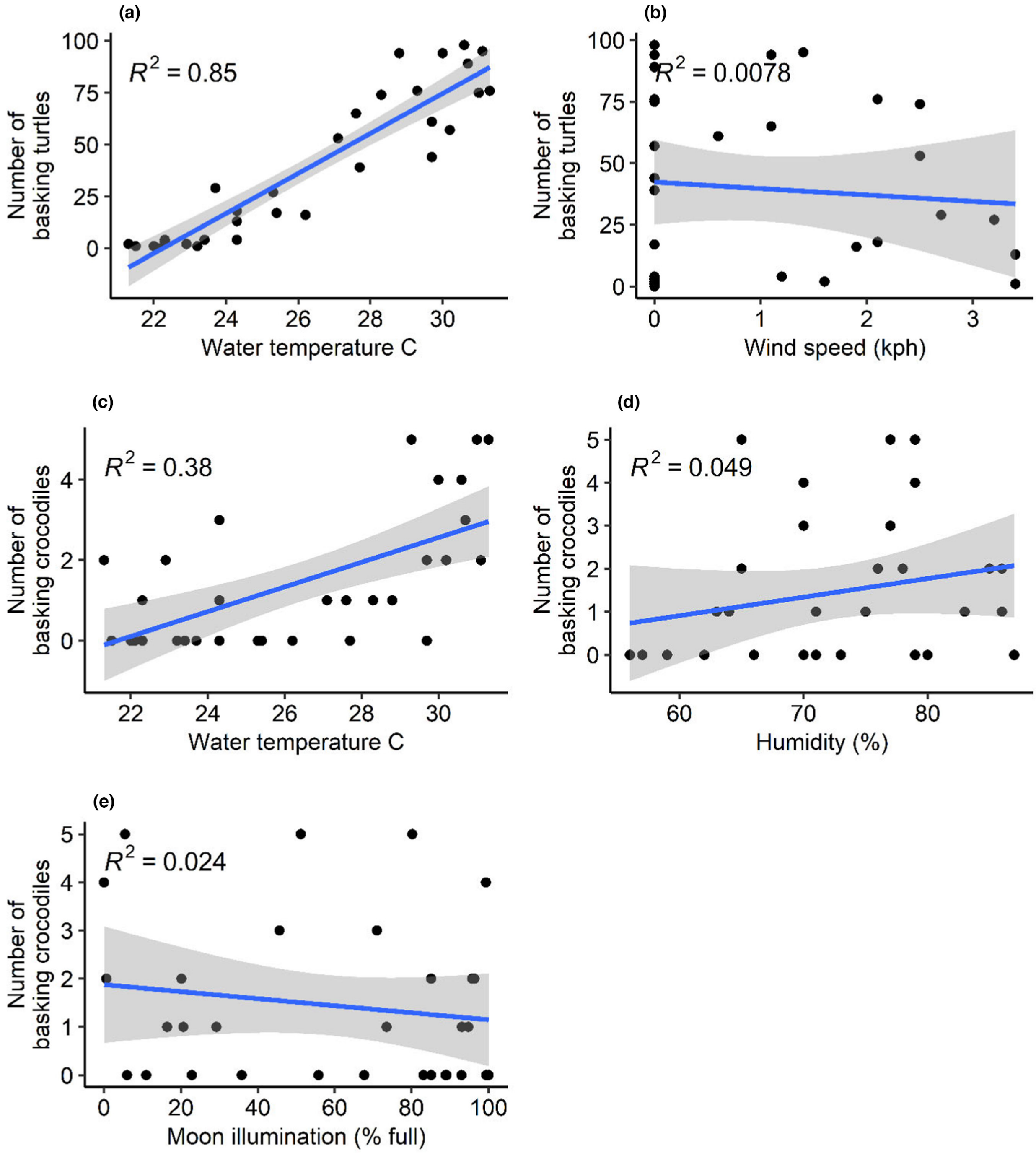

FIGURE 4 Number of nocturnally basking individuals (turtles [a, b] and crocodiles [c, d, e]) per survey regressed against the environmental variables in the best-fit models. Shading indicates 95% confidence intervals.

in other important factors (e.g., temperature) during those surveys. Therefore, to better assess the influence of wind speed on nocturnal basking activity, we also ran model selection including only surveys with wind speed greater than 0. This process reduced the amount of data available in the model but did not change the result for turtles (Tables S1 and S2; water surface temperature remained the only significant factor; Figure S1). Data for crocodiles changed slightly (Tables S1 and S2) and water surface temperature and humidity were both significant factors (Figure S1).

TABLE 3 Model selection results show our top 5 models for each species including environmental variables of importance. Model ranks are scored by the lowest AICc values.

Species	Model rank	Terms in model	Df	Log-likelihood	AICc	ΔAIC	Weight
Emydura macquarii krefftii	1	Water temp	3	−124.364	255.6	0.00	0.426
	2	Water temp Wind speed	4	−123.839	257.2	1.60	0.191
	3	Water temp Humidity	4	−124.235	258.0	2.39	0.129
	4	Water temp Moon illumination	4	−124.351	258.2	2.62	0.115
	5	Water temp Wind speed Humidity	5	−123.734	260.1	4.25	0.051
Crocodylus johnstoni	1	Water temp Humidity	3	−42.129	91.1	0.00	0.332
	2	Water temp	2	−43.846	92.1	0.97	0.204
	3	Water temp Moon illumination Humidity	4	−41.462	92.5	1.32	0.172
	4	Water temp Humidity Wind speed	4	−42.106	93.8	2.60	0.090
	5	Water temp Moon illumination	4	−43.575	94.0	2.89	0.078

TABLE 4 Generalized linear model results with significant p values listed in bold (response = the number of animals basking, distribution for *E. m. krefftii* = Guassian; *C. johnstoni* = Poisson).

Species	Terms in model	95% CI	χ^2	P-value
Emydura macquarii krefftii	Water temp	8.157–11.204	169.409	**<0.001**
	Wind speed	−2.263 – 6.431	0.964	0.326
Crocodylus johnstoni	Water temp	0.132–0.359	4.239	**<0.001**
	Humidity	−0.004 – 0.078	1.782	0.075
	Moon illumination	−0.014 – 0.004	1.110	0.267

Influence of temperature

The surface temperature of the water played an important role in predicting the frequency of nocturnal basking events for both turtles and crocodiles (see above). Both turtles and crocodiles basked more frequently at night during surveys when the water temperature exceeded the air temperature. However, the magnitude of this difference was less important than the temperature of the water (i.e. nocturnal basking was most common when the water surface temperature was simultaneously high in absolute terms and higher than the air temperature, whereas it was less common if the water surface temperature was low in absolute terms even if it was higher than the air temperature; Figure 5). Both turtles and crocodiles basked more at night when the water temperatures were high and 3–5°C above the air temperature. During cooler months (blue points; Figure 5), both turtles and crocodiles were less likely to bask at night even if the water was much warmer than the air.

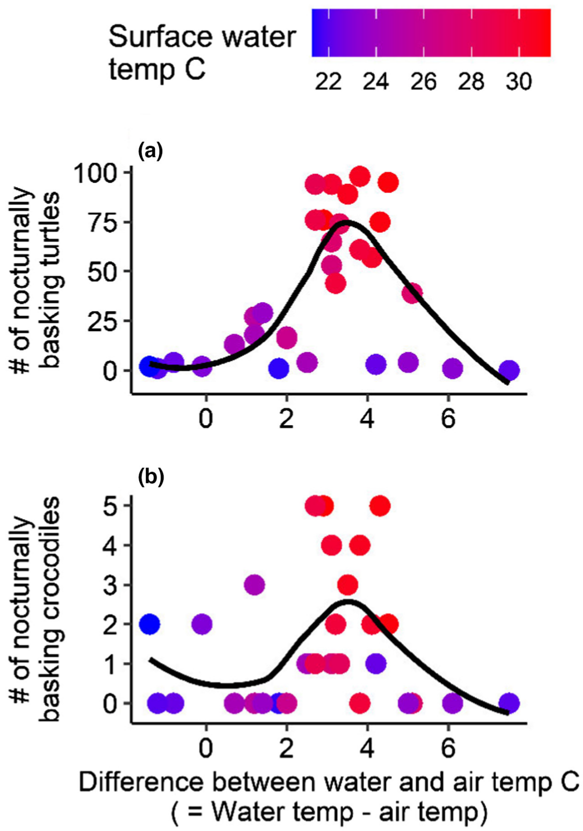

FIGURE 5 The number of nocturnally basking turtles (*Emydura macquarii krefftii*; a) and crocodiles (*Crocodylus johnstoni*; b) relative to the difference between the water surface temperature and air temperature. The x-axis represents the number of degrees (c) that the water was warmer than the air, whereas the shading represents the absolute water temperature. The black line is a smoothed, polynomial regression line constructed using geom_smooth() in the ggplot2 package (Wickham, 2016).

DISCUSSION

This study is the first to examine seasonal patterns of nocturnal basking in turtles and among the first to look for seasonal patterns of nocturnal basking in crocodiles. Our study indicated that nocturnal basking was a common behaviour for *E. m. krefftii* and *C. johnstoni*, with strong ties to seasonality. Both taxa basked at night throughout the year, but there was a strong seasonal effect, for both taxa, with greatly reduced nocturnal basking activity when air temperatures were low during winter months. Similarly, water surface temperature was an important predictor of nocturnal basking, with increased basking activity on nights with high water surface temperature. Taken together, these results suggest that nocturnal basking is likely influenced by temperature, at least to some level, which we describe below.

As ectotherms, body temperatures are highly influenced by environmental conditions, therefore, selecting a microclimate with temperatures within a preferred temperature range should facilitate thermoregulation. The Ross River is a tropical river system that maintains high water temperatures during the summer months, which may drive turtles and crocodiles to seek lower temperature microclimates by crawling out of the water at night. For example, during surveys when the water surface temperature exceeded 28°C, it was common to observe 50 to 100+ turtles basking at night throughout the transect. In contrast, when water surface temperatures were below 24°C, nocturnal basking was rare (Figure 4a). Further, we found the interaction between the water surface and air temperatures to be important; we found increased nocturnal basking activity from both turtles and crocodiles when both the water surface temperature was high (~28°C or higher) and the air temperature was a few degrees lower (Figure 5). The magnitude of the difference between the water and air temperature was less important, given that even when the water was more than 6°C higher than the air temperature during winter, both turtles and crocodiles would not bask at night, likely because the air temperature was not within their preferred temperature range. A recent experimental, lab-based study by Kidman et al. (in press—this issue), established a thermal preference of 26°C in this population of *E. m. krefftii* and found increased nocturnal basking activity when water temperatures exceeded that thermal preference. That result agrees strongly with our field-based data, with most nocturnal basking occurring when the water was >26°C and when the air temperature was lower than the water temperature (Figures 4 and 5).

Remaining in water above-preferred temperature ranges, even while resting, is metabolically costly (Spencer et al., 1998) and by engaging in nocturnal basking, turtles and crocodiles could reduce their body temperatures (and therefore metabolic expenditure) through evaporative cooling on nights when the air temperature is below the water surface temperature. While some physiological processes are increased with higher body temperatures (e.g. food assimilation by *Emydura macquarii* was faster at 30°C than at 20°C; Spencer et al., 1998) prolonged exposure to high body temperatures can also be detrimental, resulting in unnecessary energy expenditure. Although river systems often support diverse water temperatures with thermoclines, the Ross River is slow-moving and only 3–4 m deep (most sections 2–3 m), with only a slight thermocline present in the warmer months (Nordberg and McKnight, unpublished data), so animals may be unable to easily achieve optimal temperatures while in the water.

Field studies with temperature-sensitive data loggers on free-range turtles in this population would provide valuable data in this system to fill this knowledge gap. Manning and Grigg (1997) conducted such a field study and found *E. macquarii* [*E. signata*] were thermoconformers and did not thermoregulate via basking. However, their study was conducted approx. 10 degrees of latitude further south (1000 km; near Brisbane, Australia) than our study. Further, Manning and Grigg (1997) do not report nocturnal basking in their study, which may not be a common behaviour in that population. Because *E. macquarii* have a large range across eastern Australia, populations are subject to very different environmental conditions. For example, in Manning and Grigg (1997), average water temperatures ranged from 13°C in winter to 27°C in summer, whereas in our study in the Ross River, water surface temperatures ranged from 19°C in winter to 34°C in summer (Nordberg and McKnight, unpublished data).

Several other hypotheses for nocturnal basking have been proposed, such as resting, predator avoidance and parasite removal (Barhadiya et al., 2020; Nordberg & McKnight, 2020). However, none of them can adequately explain the behaviour in this system. First, if any of these factors were driving the behaviour, we would not expect to see such strong associations with temperature. Further, it is unclear why animals would need to rest out of the water in the Ross River because, due to a series of weirs, it is nearly stagnant, with very little flow. Likewise, adult crocodiles have no predators in this system (and therefore nothing to avoid). Adult turtles in the Ross River have few predators, and basking may actually increase their risk of predation (due to increased exposure to avian predators) rather than decreasing it. Indeed, the only obvious aquatic predator of adult turtles in the Ross River is *C. johnstoni*, but we frequently saw *E. m. krefftii* basking beside or even on top of *C. johnstoni*, thus making basking a poor strategy for avoiding crocodiles. Finally, a previous study (McKnight et al., 2021) tested the hypothesis that *E. m. krefftii* in the Ross River basked nocturnally to remove parasites and found that despite having high initial leech loads, basking for three consecutive hours at night had no effect on the leech loads of 11 turtles and only resulted in a loss of one and four leeches from two other turtles.

Taken together, we argue that the current evidence suggests that nocturnal basking may facilitate thermoregulatory cooling by emerging from unfavourably high water temperatures. However, the scope of this study did not allow for the collection of body temperatures on basking individuals, and using temperature-sensitive transmitters or temperature loggers on free-ranging individuals in this population would be a valuable next step to test body temperature regulation.

Beyond the seasonal and temperature patterns, we found the effects of structure availability and anthropogenic influences on nocturnal basking frequency. Nocturnally basking turtles and crocodiles were not distributed uniformly across the study area and, unsurprisingly, were concentrated in the areas with the highest amount of basking habitat. However, even after controlling for structure availability, both species exhibited a preference for the east (bushland) side of the river, rather than the western bank that consists of houses and lawns. This result suggests avoidance of human activity and is consistent with previous work on diurnal basking habits which report that anthropogenic activities reduce basking frequency (Lambert et al., 2013; Moore & Seigel, 2006; Pittfield & Burger, 2017). Decreased basking frequency or duration caused by human activity has physiological implications and suggests that human encroachment on waterfronts may be interfering with aquatic reptiles' basking habits, including thermoregulation—a vital behaviour influencing physiological responses. Diurnal basking allows reptiles to attain body temperatures that increase digestion, gamete production, metabolism and overall fitness (Angilletta, 2009; Beaupre et al., 1993; Huey, 1982). Therefore, adequate availability of basking structures is necessary for animals to attain optimal temperatures for many of these functions. Maintaining thermal heterogeneity and suitable basking structures is especially important for gravid females, which increase diurnal basking activity to increase the development of oviductal eggs in preparation for nesting (Krawchuk & Brooks, 1998; Lefevre & Brooks, 1995). Nocturnal basking, conversely, may be important for avoiding overheating and wasted energy expenditure from exposure to temperatures that are higher than optimal. More work is needed to understand the physiological role of this behaviour and the potential for human activities to interrupt it.

In summary, we identified seasonal patterns in the nocturnal basking habits of both turtles and crocodiles and speculate that this behaviour is used to escape unfavourably warm water temperatures. Additionally, we found evidence that this behaviour is more common on riverbanks with less human disturbance. Future work should test the efficacy of body temperature regulation in individuals that engage in nocturnal basking and examine the possible conservation implications of these results, particularly given the increasing temperatures from anthropogenic climate change and the continual encroachment of humans on aquatic environments.

AUTHOR CONTRIBUTIONS

Eric J. Nordberg: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (lead); project administration (equal); resources (lead); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Donald McKnight:** Conceptualization (equal); data

curation (equal); formal analysis (equal); investigation (equal); methodology (supporting); writing – original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made available in the Dryad repository upon publication.

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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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