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Nocturnal basking in freshwater turtles: A global assessment

Donald T. McKnight^{a,*}, Kendall Ard^b, Renoir J. Auguste^c, Gaurav Barhadiya^d, Michael F. Benard^e, Paige Boban^f, Martin L. Dillon^g, Colleen T. Downs^h, Brett A. DeGregorioⁱ, Brad M. Glorioso^j, Rachel M. Goodman^k, Coen Hird^l, Ethan C. Hollender^m, Malcolm Kennedyⁿ, Rosie A. Kidman^o, Andrhea Massey^m, Pearson McGovern^p, Max Mühlenhaupt^q, Kayhan Ostovar^b, Danusia Podgorski^r, Cormac Price^h, Beth A. Reinke^f, Louise M. Streeting^o, Jane Venezia^e, Jeanne Young^r, Eric J. Nordberg^{o,s}

^a Department of Environment and Genetics, School of Agriculture, Biomedicine and Environment, La Trobe University, Wodonga, Victoria 3690, Australia

^b Department of Math and Science, Rocky Mountain College, Billings, MT 59102, USA

^c Department of Life Sciences, The University of the West Indies, St. Augustine, Trinidad and Tobago

^d Department of Environmental Studies, University of Delhi, New Delhi 110007, India

^e Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA

^f Department of Biology, Northeastern Illinois University, Chicago, IL 60625, USA

^g Northern Tablelands Local Land Services, Armidale, New South Wales 2350, Australia

^h Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa

ⁱ US Geological Survey, Fish and Wildlife Cooperative Research Unit, University of Arkansas, Fayetteville, AR 72701, USA

^j US Geological Survey, Wetland and Aquatic Research Center, 700 Cajundome Blvd., Lafayette, LA 70506, USA

^k Biology Department, Hampden-Sydney College, Hampden-Sydney, VA 23901, USA

^l School of Biological Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

^m Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

ⁿ Department of Agriculture and Fisheries, 203 Tor St, Toowoomba, Queensland 4350, Australia

^o Department of Zoology, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia

^p African Chelonian Institute, Ngazobil, 23015 Thies, Senegal

^q Department of Behavioural Ecology, Bielefeld University, Konsequenz 45, Bielefeld 33615, Germany

^r College of Science and Engineering, Flinders University, Bedford Park, South Australia 5042, Australia

^s College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia

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ABSTRACT

Diurnal basking (“sunning”) is common in many ectotherms and is generally thought to be a behavioural mechanism for thermoregulation. Recent studies have reported the occurrence of nocturnal basking in a few distantly-related species of freshwater turtles, but the true extent of this behaviour is unknown, and it may be underreported due to sampling biases (e.g., not surveying for turtles at night). Therefore, we initiated a global, collaborative effort to systematically document and quantify basking activity (diurnal and nocturnal) across a wide range of freshwater turtle species and locations. We conducted camera trap or manual surveys in North America, the Caribbean, Europe, Asia, Africa, the Seychelles, and Australia. We collected 873,111 trail camera photographs (25,273 hrs of search effort) and obtained data on 29 freshwater turtle

* Corresponding author.

E-mail address: donald.mcknight@my.jcu.edu.au (D.T. McKnight).

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species from seven families. Nocturnal basking was documented in 13 species, representing six families (Chelidae, Emydidae, Geoemydidae, Kinosternidae, Pelomedusidae, and Trionychidae), including representatives in Central America, Trinidad and Tobago, Africa, the Seychelles, Asia, and Australia. Nocturnal basking was restricted to tropical and sub-tropical locations, suggesting that environmental temperature plays a role in this behaviour. However, the primary factors driving nocturnal basking are yet to be determined and may vary geographically and by species. The frequency and duration of nocturnal basking varied among species and seasons, but nocturnal basking events were often substantially longer than diurnal events. This is the first study to document a widespread occurrence of nocturnal basking, and our results suggest that nocturnal basking may be a common, although overlooked, aspect of many species' ecology.

1. Introduction

For species that cannot produce their own body heat (i.e., ectotherms), behavioural thermoregulation, achieved by adjusting body posture and shuttling between different environmental conditions, is required to maintain preferred body temperatures and enable optimal rates of physiological responses (e.g., digestion, metabolism, gamete production, growth, and maintenance; Congdon, 1989; Cowles and Bogert, 1944; Huey, 1982). It is also important for ecological responses, such as improved movement, vigilance, and

Table 1

Species examined. Location = country (state or region) searched. Seasons: Sp = spring, Su = summer, A = autumn, W = winter. B = basking was observed (diurnal or nocturnal), S = a site was searched but basking was not observed. Sites = total number of locations searched (proximate bodies of water were generally considered a single site). Camera hours = total hours cameras were deployed at sites where a given species was documented basking (0 = data came entirely from manual surveys or anecdotal observations). Basking events = number of basking events (nocturnal or diurnal) observed. Photos with turtles = number of photos with a basking turtle (nocturnal or diurnal). Basked at night = indicates if nocturnal basking was (Y) or was not (N) observed.

Family	Species	Location	Seasons				Sites	Camera hours	Basking events	Photos with turtles	Basked at night
			Sp	Su	A	W					
Chelidae	<i>Chelodina expansa</i>	AU (QLD)	B	S	S	S	2	3050	9	71	Y
Chelidae	<i>Chelodina longicollis</i>	AU (NSW, SA)	B	B	S	S	2	4273	11	1794	N
Chelidae	<i>Elseya irwini/ Myuchelys latisternum*</i>	AU (QLD)	-	B	-	-	1	1021	162	1682	Y
Chelidae	<i>Elseya lavarackorum</i>	AU (QLD)	-	B	-	-	1	0	-	-	Y
Chelidae	<i>Emydura macquarii</i>	AU (QLD, SA)	B	B	B	B	4	7324	3678	23585	Y
Chelidae	<i>Myuchelys bellii</i>	AU (NSW)	B	B	-	-	1	1008	351	5721	N
Chelidae	<i>Myuchelys latisternum</i>	AU (QLD)	S	B	S	S	1	1874	1	4	N
Chelydridae	<i>Chelydra serpentina</i>	US (AR, OH)	B	B	S	-	2	2930	12	335	N
Emydidae	<i>Chrysemys picta</i>	US (MT, OH, VA, WI)	B	B	B	-	4	4189	743	9024	N
Emydidae	<i>Emys orbicularis</i>	DE (BB)	B	B	-	-	2	2974	757	10969	N
Emydidae	<i>Graptemys pseudogeographica</i>	US (LA, OK)	B	-	B	-	2	1596	160	1735	N
Emydidae	<i>Pseudemys concinna</i>	US (LA, OK)	B	-	B	-	2	1596	99	2361	N
Emydidae	<i>Trachemys scripta</i>	AU (QLD), TT (CTTRC), US (AR, OK, LA)	B	B	B	B	6	9048	603	16127	N
Emydidae	<i>Trachemys venusta</i>	BZ (ORZ)	-	B	-	-	1	134	53	1191	Y
Geoemydidae	<i>Pangshura smithii</i>	IN (AS)	-	B	B	-	2	0	-	-	Y
Geoemydidae	<i>Pangshura sylhetensis</i>	IN (AS)	-	B	B	-	3	0	-	-	Y
Geoemydidae	<i>Pangshura tecta</i>	IN (AS)	-	B	B	-	3	0	-	-	Y
Geoemydidae	<i>Pangshura tentoria</i>	IN (AS)	-	B	B	-	3	0	-	-	Y
Kinosternidae	<i>Kinosternon scorpioides</i>	TT (RCM)	-	B	-	-	1	0	-	-	Y
Kinosternidae	<i>Sternotherus carinatus</i>	US (LA, OK)	B	-	B	-	2	1596	10	177	N
Kinosternidae	<i>Sternotherus odoratus</i>	US (AR)	S	S	B	-	1	1922	1	7	N
Pelomedusidae	<i>Pelomedusa galeata</i>	ZA (KZN)	-	B	-	B	1	1113	131	1578	N
Pelomedusidae	<i>Pelusios adansonii</i>	SN (TH)	-	B	-	S	1	336	33	2391	Y
Pelomedusidae	<i>Pelusios castanoides</i>	SC (SI)	B	B	B	B	1	0	-	-	Y
Pelomedusidae	<i>Pelusios subniger</i>	SC (SI)	S	S	S	S	1	0	-	-	N
Trionychidae	<i>Apalone spinifera</i>	US (AR, MT, OK)	B	B	S	-	3	4111	636	2238	N
Trionychidae	<i>Nilssonina gangetica</i>	IN (AS)	-	B	B	-	3	0	-	-	Y
Trionychidae	<i>Nilssonina hurum</i>	IN (AS)	-	B	B	-	3	0	-	-	N * *
Trionychidae	<i>Nilssonina nigricans</i>	IN (AS)	-	B	B	-	3	0	-	-	N * *

Countries: AU = Australia, BZ = Belize, DE = Germany, IN = India, SC = Seychelles, SN = Senegal, TT = Trinidad and Tobago, US = United States of America, ZA = South Africa. **States or regions:** AS = Assam, AR = Arkansas, BB = Brandenburg, CTTRC = Couva-Tabaquite-Talparo, LA = Louisiana, MT = Montana, KZN = KwaZulu-Natal, NSW = New South Wales, OH = Ohio, OK = Oklahoma, ORZ = Orange Walk, RCM = Rio Claro-Mayaro, SA = South Australia, SI = Silhouette Island, TH = Thies, QLD = Queensland, VA = Virginia, WI = Wisconsin. *Both species were observed but it was often not possible to distinguish them. * *Nocturnal basking was not observed in the present study but was reported in Barhadiya et al. (2020).

predator avoidance (Christian et al., 2016; Huey, 1982; Spencer et al., 1998). Diurnal basking (i.e., resting on exposed structures such as rocks and logs) is a common behavioural trait that ectotherms, particularly reptiles, use to control body temperature (Hertz et al., 1993; Huey, 1982).

Basking is frequently observed in freshwater turtles, which often leave the water to absorb solar radiation. While basking in freshwater turtles is primarily thought to aid in thermoregulation (Auth, 1975; Boyer, 1965; Crawford et al., 1983; Moll and Legler, 1971; Obbard and Brooks, 1979; Schwarzkopf and Brooks, 1985), not all studies have found evidence that it is thermoregulatory (Manning and Grigg, 1997), and there are many additional hypotheses about its benefits. For example, multiple studies have proposed that basking may reduce ectoparasite loads, such as leeches (Ibáñez et al., 2014; McAuliffe, 1977), and there is some evidence that it can act as a form of behavioural fever to fight off infection (Monagas and Gatten, 1983; Rakus et al., 2017; Wirth and Ariel, 2020). However, a recent study failed to show a significant reduction in leech loads after experimentally inducing basking (McKnight et al., 2021). Other studies have suggested that basking may help dry out the carapace (Chessman, 1987), which could reduce algal accumulation and fungal growth (Boyer, 1965; Bury et al., 2015; Garbary et al., 2007) or facilitate scute shedding (Boyer, 1965; Neill and Allen, 1954). Further hypotheses include resting (Boyer, 1965) and increased UV absorption (Acierno et al., 2008; Bos et al., 2018; Bouazza et al., 2016; Conley and Lattanzio, 2022). There is still much to learn about this behaviour, and many of these hypotheses are not mutually exclusive, so there may be multiple context-dependent drivers.

Despite the apparent importance of basking behaviour, it was only recently documented that some wild turtles frequently engage in “nocturnal basking” (i.e., exiting the water at night to sit on structures such as logs and rocks, often for extended periods of time; Barhadiya et al., 2020; Nordberg and McKnight, 2020). This behaviour had previously gone unrecorded despite occurring within a

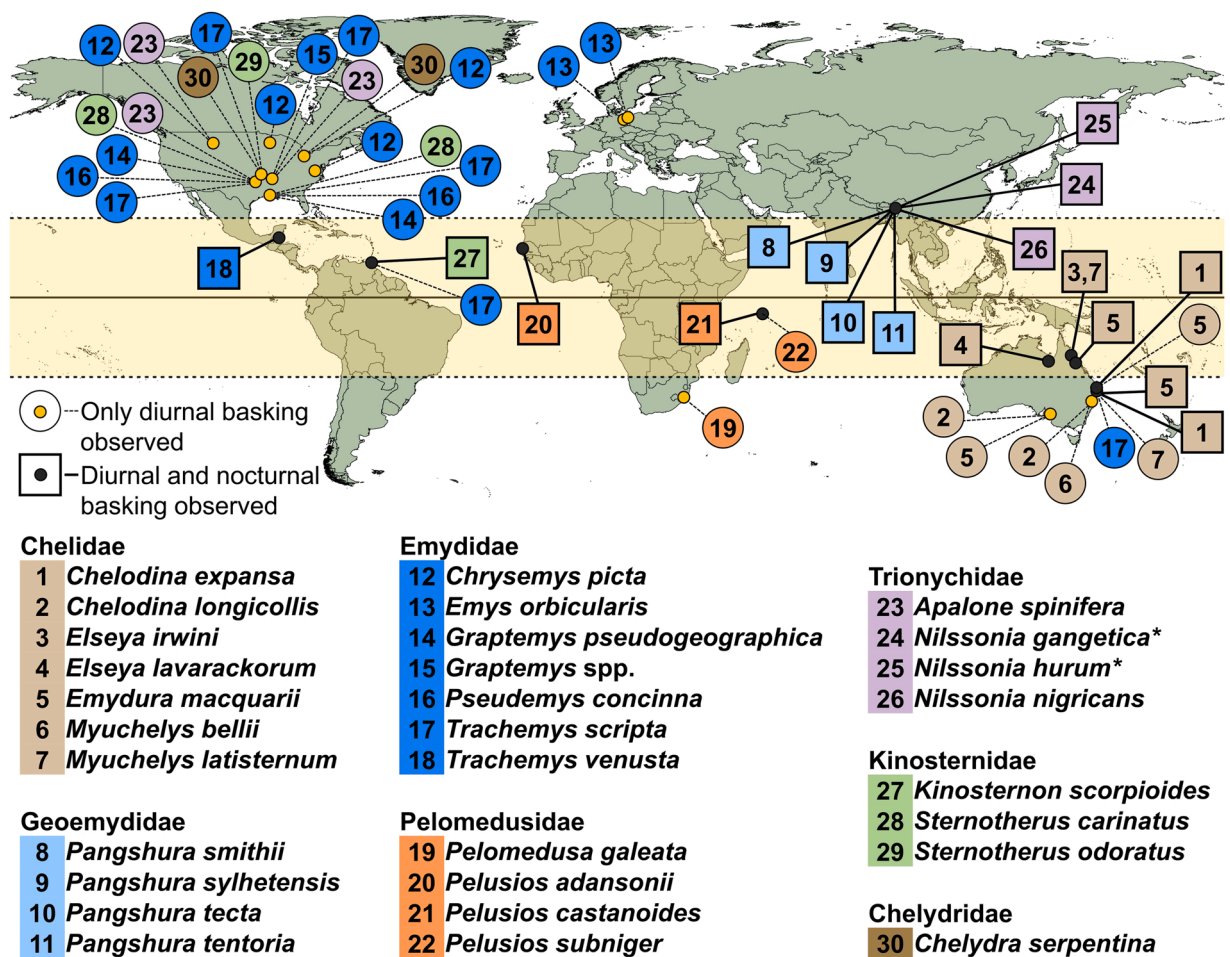


Fig. 1. Map showing the species and study sites sampled. Sites are represented as yellow or black dots (depending on whether nocturnal basking was documented at that site), and species per site are represented as large, numbered circles (only diurnal basking was observed) or squares (diurnal and nocturnal basking was observed). The equator is shown as a solid line, and the tropics are highlighted in transparent yellow. Note that all three temple ponds in India are shown as a single point (with the exception of *P. smithii* [two ponds] all species were observed at all three ponds). Two species denoted by * were observed basking at night by Barhadiya et al. (2020) but were not observed basking at night in the current study. *Elseya irwini* and *Myuchelys latisternum* were listed together at one site because it was generally not possible to distinguish them, and it is not clear which species was basking at night (possibly both).

major urban area (Nordberg and McKnight, 2020). This raises the possibility that the behaviour may be widespread and simply undocumented because of a lack of search effort at night. Further, the function of nocturnal basking is presently unknown, but may represent an important aspect of some species' ecology.

To help fill these knowledge gaps, we conducted a systematic, international assessment of basking activity in freshwater turtles. We designed a protocol to record basking activity through remote, time-lapse wildlife camera deployments around the world. We also incorporated manual surveys when remote camera deployments were not feasible or available to researchers. While our primary goals were to examine the geographic and taxonomic extent of nocturnal basking, we also collected valuable data on diurnal basking to further our understanding of that important behaviour.

2. Methods

2.1. Study subjects

We collected basking observations on 29 species of freshwater turtle representing seven of the 11 extant freshwater turtle families (Table 1; Fig. 1). Three of the remaining freshwater families (Carettochelyidae, Dermatemydidae, and Platysternidae) are monotypic.

2.2. Study sites

We collected data from Africa, Asia, Australia, Central America, Europe, North America, the Seychelles, and Trinidad and Tobago (in the Caribbean); however, most of the data came from Australia and North America (Table 1; Fig. 1). Study site details are available in the [Supplemental Information](#).

2.3. Data collection

In most cases, a minimum of three wildlife trail camera traps, set to time-lapse mode (two-minute photograph interval) with an infrared flash, were positioned at different basking structures (e.g., rocks, logs, muskrat [*Ondatra zibethicus*] lodges, artificial basking platforms, or riverbanks) within an area (river, series of ponds, etc.) to record basking behaviours for seven consecutive days (a total of 21 camera-trap-days of recordings). Each 21-day block of recordings was repeated at least once (a minimum of a month apart; in two different seasons when possible) to account for temporal variation. Camera traps usually were oriented at the same basking structures in all repeated time-period blocks. In some cases, variations on this protocol were used based on the availability of study sites, basking structures, and camera traps (e.g., number of cameras per site ranged from 1 to 5 [mean = 3.2], seasons surveyed per site ranged from 1 to 4 [mean = 2.1], camera deployments per site per season ranged from 1 to 4 [mean = 1.5], and sometimes several small, proximate bodies of water were surveyed rather than placing multiple cameras at a single waterbody; see Table 1 and the [Supplemental Information](#) for details of the methods used at each site). In most cases, wild populations were studied, but for *Pelusios adansonii*, *Pelusios castanoides*, *Pelusios subniger*, and one population of *Emys orbicularis*, turtles in large, naturalised, outdoor, captive enclosures were used (see [Supplemental Information](#) for details). For all camera traps, we recorded the number of turtles basking in each photograph (these data were used only to document which species basked nocturnally and diurnally at each site), and for at least one camera trap per site per season, we recorded the time of the first and last photograph in which a given turtle was observed, thus providing a duration (these data are referred to as "basking events" and were used in visualisations and analyses; note that individuals were not identified and some individuals may have been recorded multiple times during different basking events). Any occurrence of turtles emerging from and sitting out of the water was defined as "basking" (minimum photo interval was generally 2 min, which also, therefore, was the minimum basking duration). Note that even for the longest basking events, individuals sat relatively still rather than pacing, foraging, or engaging in other behaviours that were clearly distinct from basking. We also noted potential predators at each site (both observed on cameras or known to be in the area) and reported them in the [Supplemental Information](#).

Additionally, at three large, naturalistic, outdoor temple ponds in India, it was not possible to use camera traps. Therefore, all three ponds were manually surveyed for basking turtles on seven days and nights in the summer and autumn. For consistency with camera trapping methods (three cameras deployed in an area), all three temple ponds were treated as a single site for analyses unless otherwise noted (with the exception of *Pangshura smithii* [two ponds] all species were observed at all three ponds). A site in Belize was also surveyed manually for five nights during the summer in addition to a single camera trap deployment. Finally, in several instances, anecdotal observations were made. Headlamps were used for manual surveys and anecdotal observations. In many cases this did not appear to disturb turtles, and when turtles did flee, we were usually able to identify and count the turtles before they fled. Details on the data collection methods at each site are outlined below (Sections 3.3 and 3.4), with more detailed descriptions available in the [Supplemental Information](#).

2.4. Data analyses

Because of the complex nature of the data (multiple sites, species, and seasons, with varying levels of overlap among those factors) we were limited in our ability to run valid statistical models. Therefore, some results are presented descriptively rather than statistically. However, there were some cases where statistical analyses were possible. Data were generally grouped or summarised by species per site per season (species/site/season), and unless otherwise noted, only species/sites/seasons with ≥ 30 basking events were included in statistical analyses.

Several analyses and visualisations used percent of basking activity per hour. This was calculated per species/site/season as the total minutes of basking per hour divided by the sum of the durations of all basking events. These analyses and visualizations were designed to examine peak times of basking activity rather than simply examining binary categories of “nocturnal” and “diurnal.” Because differences in the timing of sunrise and sunset across latitudes and time zones could confound results, unless otherwise noted, we standardised these data relative to the midpoint of sunrise and sunset for each site/season. Thus 0 = the midpoint between sunrise and sunset, - 1 = an hour before the midpoint, 1 = an hour after the midpoint, etc. This allowed more meaningful comparisons, because 0 was always the time when the sun was at its zenith for all species/sites/seasons. These standardized data were used for the subset of analyses that specifically targeted diurnal basking behaviour.

We conducted all analyses in R (v4.0.3; R Core Team, 2020). We constructed all mixed effects models (described below) with the

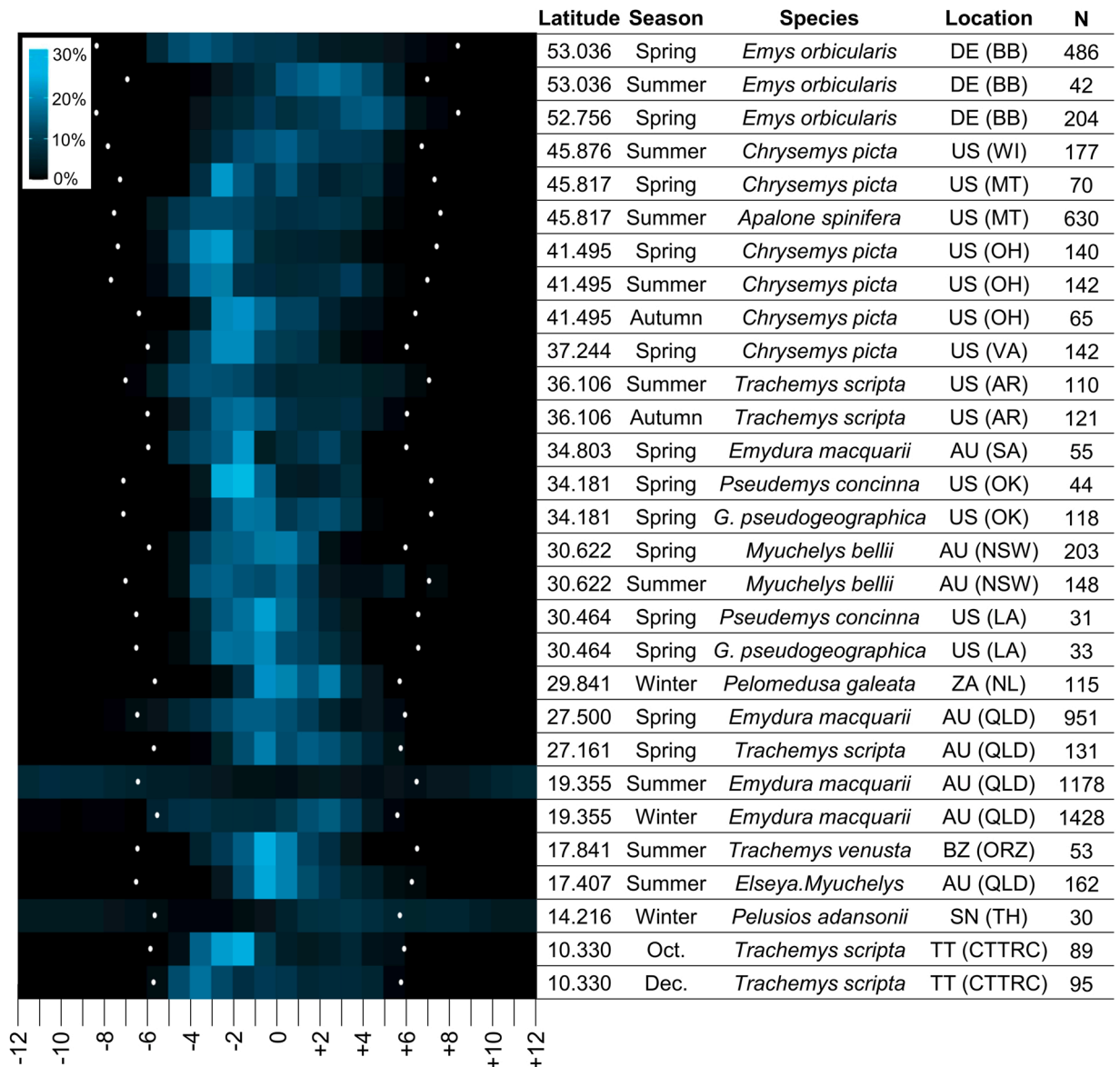


Fig. 2. Daily basking activity patterns (for species/sites/seasons with ≥30 basking events detected on camera traps) represented as a heatmap showing the percent of freshwater turtle basking activity that occurred within each hour (i.e., each block is the sum of the amount of time turtles spent basking in that hour divided by the total amount of time basking for that species/site/season). 0 = the midpoint of sunrise and sunset, and each tick represents 1 h. Data are ordered by the absolute value of the latitude. White dots indicate sunrise and sunset times at a given site/season (row). Note that in four cases, cameras were deployed multiple times within a season, and the midpoint of sunrise or sunset times is shown (sometimes resulting in slight asymmetry). Location = country (state or region) see Table 1. N = number of basking events. *G. pseudogeographica* = *Graptemys pseudogeographica*; *Elseya irwini* and *Myuchelys latisternum* (“*Elseya.Myuchelys*”) were mostly indistinguishable from photos and are reported together (see Section 3.4.2). Note that both *Trachemys scripta* samples in TT were during the rainy season (October and December).

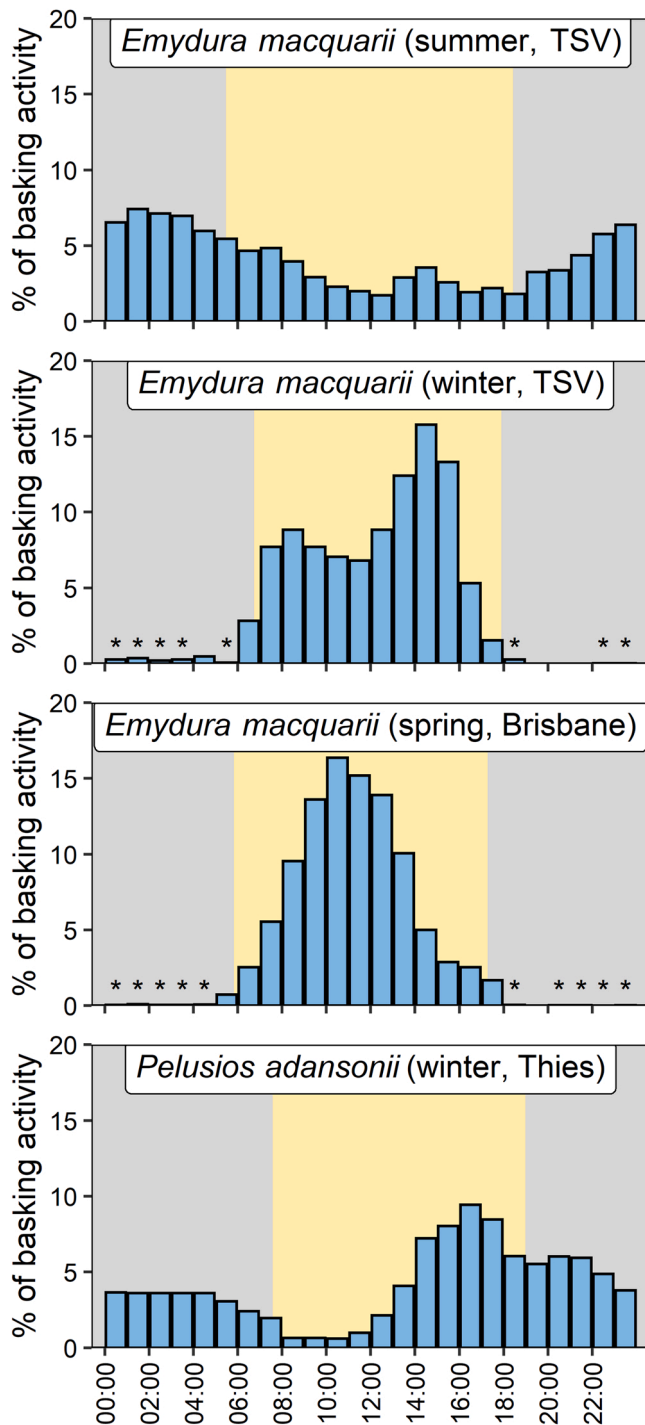


Fig. 3. Percent of all basking activity (based on the sum of minutes of basking) that occurred in each hour for species/sites that basked at night and had ≥ 30 data points. Day and night are indicated by yellow and grey shading, respectively (times were not shifted to midday because local sunrise and sunset times are shown). * = nocturnal basking was observed but constituted $< 0.5\%$ of basking activity. TSV = Townsville, Australia.

lme4 package (v1.1–26; Bates et al., 2015) and assessed significance with the Anova function and type II sum of squares via the car package (v3.1–0; Fox and Weisberg, 2019).

2.5. Latitudinal effect on nocturnal basking

We used a binomial mixed effects model to examine latitudinal trends in nocturnal basking. For this model, each species/site was entered as a data point (regardless of number of basking events, method of data collection, or season), with a binomial variable indicating whether that species was ever observed basking at night as the response, the absolute value of the latitude of the study site as a fixed effect, and species as a random intercept. We ran this model both with and without captive populations (the data from temple ponds were treated as captive data). For both models, we compared Akaike Information Criterion (AIC) values of different link functions to identify the best fit. We ran the final analyses using “logit” for the model with all species and “cloglog” for the model excluding captive turtles. It should be acknowledged that these analyses assumed that a failure to detect nocturnal basking was evidence of a true lack of nocturnal basking for a given species/site; however, our extensive camera trapping efforts should have minimized the risk of false negatives.

2.6. Duration of nocturnal basking vs diurnal basking

For *Emydura macquarii*, sufficient nocturnal and diurnal data were collected to statistically compare the average duration of diurnal and nocturnal basking events. We used Wilcoxon-Mann-Whitney-U tests and conducted a separate test for each site/season.

2.7. Latitudinal effects on diurnal basking

We used three linear mixed effects models to test effects of latitude on the duration, timing, and concentration of diurnal basking (model assumptions were checked with QQ plots and residual plots). All three models used turtle species as a random intercept and included season (spring, summer, autumn, winter) and the absolute value of the latitude as fixed effects. Season should be viewed as a blocking variable rather than an actual test of seasonal patterns because few species had ≥ 30 basking events at a site over two seasons

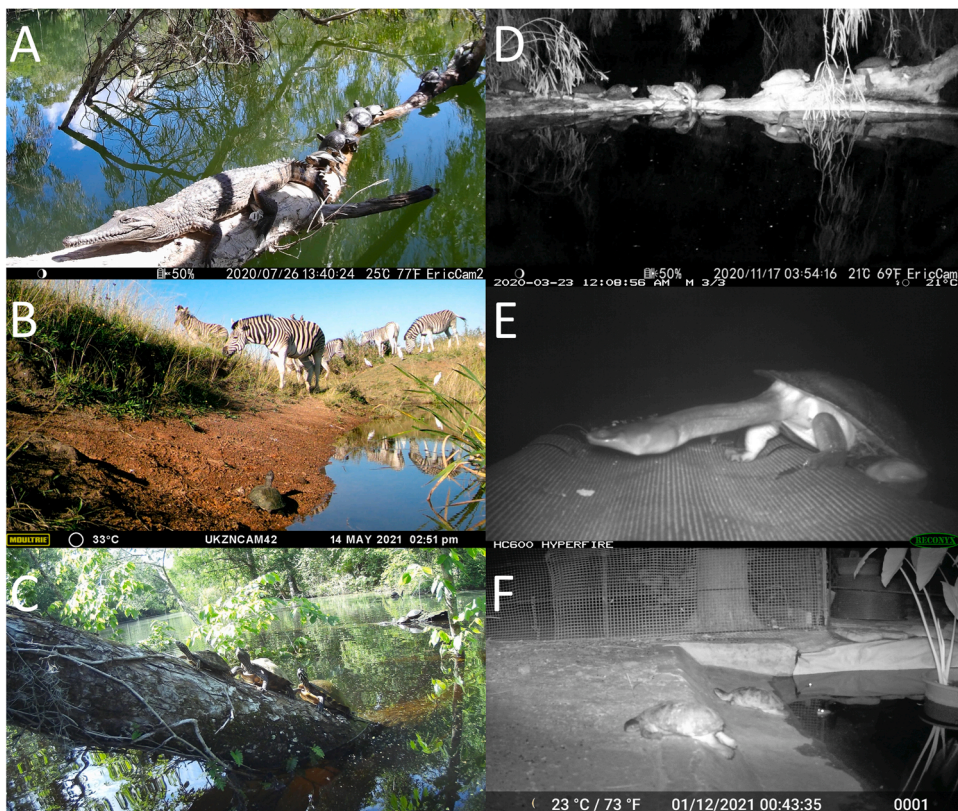


Fig. 4. Diurnal (A-C) and nocturnal basking (D-F) in freshwater turtles. A and D = *Emydura macquarii* (plus *Crocodylus johnstoni*; Australia. Photos by Eric Nordberg used with permission). B = *Pelomedusa galeata* (South Africa. Photo by Cormac Price used with permission). C = Several Emydidae species (United States of America. Photo by Brad Glorioso used with permission). E = *Chelodina expansa* (Australia. Photo by Malcolm Kennedy used with permission). F = *Pelusius adansonii* (Senegal. Photo by Pearson McGovern used with permission).

(see Section 2.8 “Seasonal timing of diurnal basking”). Because these analyses were targeted at diurnal basking questions, we limited the data to species/sites/seasons where basking behaviour occurred primarily during the day (thus *Emydura macquarii* at Townsville during the summer and *Pelusios adansonii* in winter were excluded). We did this to ensure that any potential influence of nocturnal basking on diurnal basking patterns (see Figs. 2 and 3) would not skew the results.

We constructed the basking duration model with the duration (log10 transformed minutes) of each basking event as a response variable. It included an additional random effect specifying each species/site/season to account for pseudo-replication. The timing model used the hour with the highest percentage of basking activity (“peak”) per species/site/season as the response variable. The concentration model used the percent of basking activity that occurred during the peak hour per species/site/season as the response variable.

2.8. Seasonal timing of diurnal basking

To examine seasonal patterns, we visualised the percent of basking activity per hour for each species/site/season (Figs. 2 and S1). It was not possible to run a statistically valid model across all species due to the uneven sampling across species, sites, latitudes, and seasons. However, in six cases, we collected ≥ 30 data points in each of two seasons for a given species/site, and in those six cases, we used Watson-Wheeler tests via the circular package (v4.0.3; Agostinelli and Lund, 2022) to statistically examine seasonal shifts in the timing of basking. Data were entered as the time that each basking event began (shifted so that the timepoint exactly midway between sunrise and sunset was scored as 0).

3. Results

3.1. Nocturnal basking

We documented some level of nocturnal basking in 13 of the 29 freshwater turtle species sampled, belonging to six of the seven sampled families (Chelidae, Emydidae, Geoemydidae, Kinosternidae, Pelomedusidae, and Trionychidae; Figs. 1 and 4; Fig. S2). These observations were made in Africa, Asia, Australia, Central America, the Seychelles, and Trinidad and Tobago (Figs. 1 and 5). Nocturnal basking was confined to tropical and a few sub-tropical sites, and nocturnally basking species were found significantly closer to the equator than species that did not bask at night, regardless of whether captive populations were ($\chi^2 = 4.37$, $df = 1$, $P = 0.0366$; Fig. 5) or were not included ($\chi^2 = 5.68$, $df = 1$, $P = 0.0172$). When considering all nocturnal basking events (regardless of species/season/site, $N = 322$), most events were short (median = 22 min), but there were numerous long events (range = 2–652 min; Fig. 6, Table 2). Many of the nocturnal basking observations were limited or anecdotal. Brief accounts of each species are provided below.

3.2. Nocturnal basking: wildlife camera trap surveys

3.2.1. *Chelodina expansa* (Chelidae; Australia)

Wild *C. expansa* were observed basking via camera traps at two artificial lakes/ponds. They basked infrequently and only nine basking events were observed, but two of them took place at night. One event (spring [October]) lasted 8 min and the other (summer [January]) lasted 14 min. The seven diurnal events lasted for 2–40 min (mean = 12.1, SD = 11.4, median = 9). There were few turtle predators at these sites (birds, domestic dogs [*Canis familiaris*], and potentially foxes [*Vulpes vulpes*]).

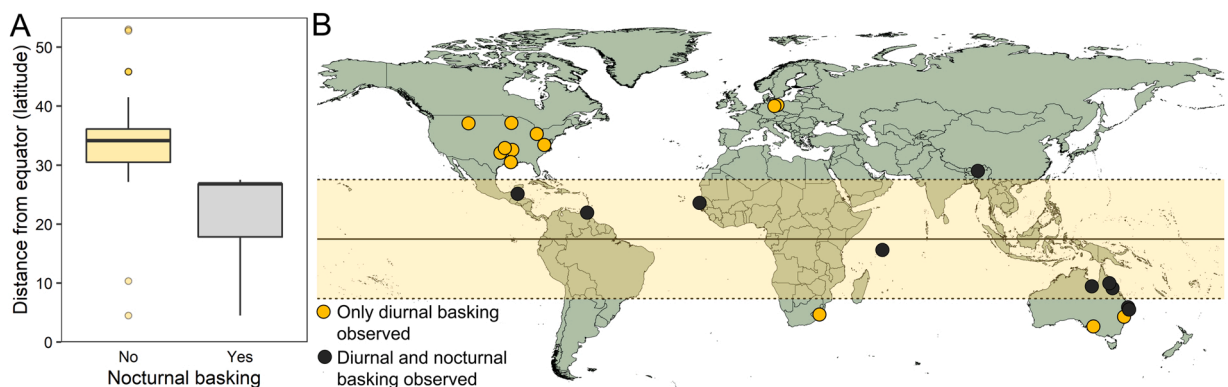


Fig. 5. Latitudinal trends in nocturnal basking in freshwater turtles. A = The absolute value of the latitude for basking observations (each species/site was included as a data point). B = Map of study locations (black points are shown if any species basked at that location at any point during the study; see Fig. 1 for species-specific details). The tropics are highlighted in transparent yellow. The boxplot was made using the default formula in ggplot2 (v3.3.6).

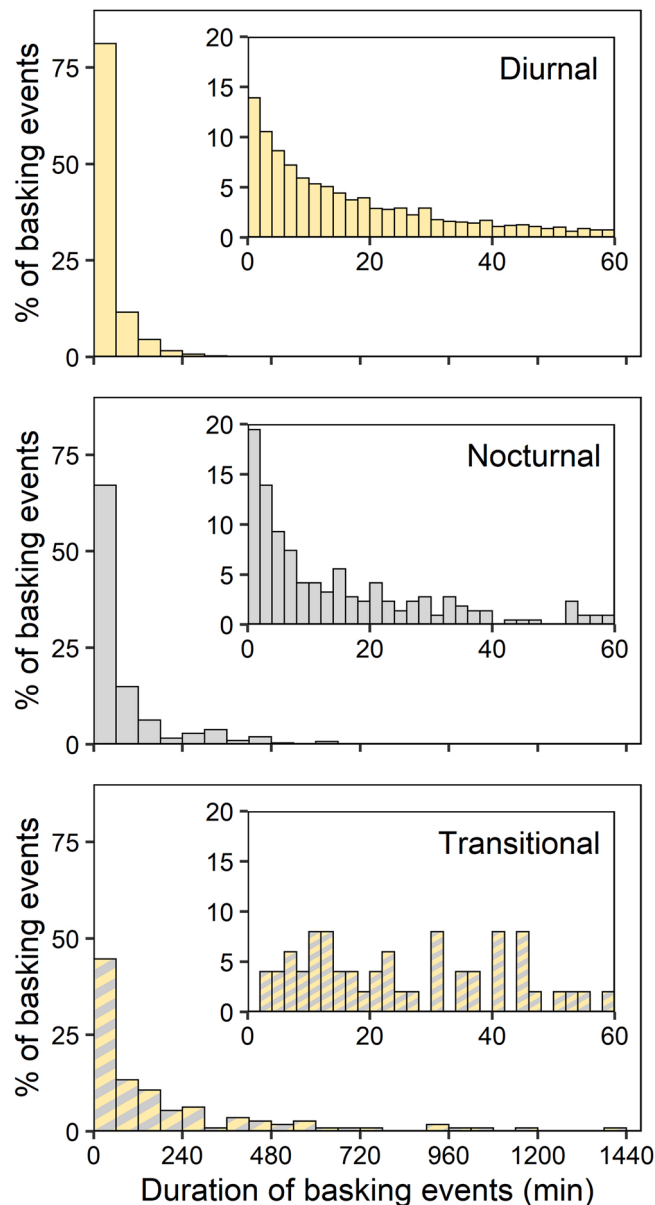


Fig. 6. Frequency distributions for durations (minutes) of basking events for freshwater turtles (across all species/sites/seasons). The inset panel shows basking events < 60 min (the first bar of the main panel) at a bin width of 2 min. Transitional = events that crossed sunrise or sunset.

3.2.2. *Emydura macquarii* (Chelidae; Australia)

Camera traps detected *E. macquarii* at four sites (three in Queensland, one in South Australia). At two sites (Ross River [Townsville] and University of Queensland Lakes [Brisbane]), nocturnal basking was observed, as well as diurnal and transitional basking events (i. e., basking events that crossed sunset or sunrise; see Table 2; Figs. 3 and 6).

In the Ross River in summer, nocturnal basking events had a significantly longer mean duration than diurnal basking events ($W = 49.073$, $P < 0.0001$). Additionally, the 55 transitional events were often relatively long (39 were > 60 min), including one that started before sunset and continued until after sunrise the next day. These events started at various times throughout the afternoon, night, and early morning. In contrast, during the winter, diurnal events were significantly longer than nocturnal events ($W = 35.797$, $P = 0.005$), and transitional events were short (compared with summer) and nearly always began shortly before sunrise (25 out of 28 [89%] began after 06:10 h). In Brisbane (spring), diurnal events were significantly longer than nocturnal events ($W = 30.601$, $P < 0.001$). The 14 transitional events were generally long and usually began shortly before sunrise, with most of the basking happening during the day (see Table 2 for durations for each site/season).

Ross River is a tropical, slow-moving river with several potential avian predators (mostly diurnal; e.g., herons, White-bellied Sea Eagles [*Haliaeetus leucogaster*], and Wedge-tailed Eagles [*Aquila audax*]), and numerous freshwater crocodiles (*Crocodylus johnstoni*).

Table 2

Basking durations (minutes) of freshwater turtles for the four cases where we were able to collect a large amount of duration data for nocturnal basking via trail cameras. Transitional = events that crossed sunrise or sunset.

Species	Location	Season	Type	N	Range	Mean	SD	Median
<i>Pelusios adansonii</i>	Theis (Senegal)	Winter	Diurnal	17	4–292	86.9	111.4	20
			Nocturnal	3	4–110	39.3	61.2	4
			Transitional	10	300–1428	835.4	373.5	949
<i>Emydura macquarii</i>	Townsville (Australia)	Summer	Diurnal	910	2–194	18.9	21.9	10
			Nocturnal	213	2–652	101.0	131.4	38
			Transitional	55	8–774	204.3	194.6	126
		Winter	Diurnal	1358	2–260	20.9	26.4	12
			Nocturnal	42	2–116	15.8	25.6	6
			Transitional	28	4–172	29.8	34.3	19
	Brisbane (Australia)	Spring	Diurnal	895	2–400	51.8	67.2	24
			Nocturnal	42	2–30	7.9	8.2	4
			Transitional	14	6–284	108.8	95.8	73

Nocturnal basking at this location has previously been reported from manual surveys (Nordberg and McKnight, 2020). The Brisbane site (1100 km further south) has few turtle predators (mostly birds).

3.2.3. *Pelusios adansonii* (Pelomedusidae; Senegal)

These observations were made at an outdoor, captive enclosure with a 3.6 m² pond and 1.9 m² concrete basking area (total enclosure size including land area = 14.9 m²). The water was only 8 cm deep during the summer (due to water restrictions from the previous dry season), which allowed females (the larger sex) to expose their carapace while in the water. The enclosure contained 19 *P. adansonii* (15 females, 3 males, 1 subadult).

Only three basking events were observed in summer (all males during the day; duration = 18, 34, and 126 min). Thirty basking events occurred in the winter, including three nocturnal basking events (duration = 4, 4, and 110 min) and ten transitional events (Table 2; Figs. 3 and 6). During these transitional events, the majority of basking took place at night (duration of nocturnal portion [min]: range = 6–756, mean = 495.1, SD = 289.9, median = 633), and in total, turtles spent more time basking at night than during the day (Figs. 2 and 3). In three cases, turtles emerged before sunset and continued basking until after sunrise the following day.

3.3. Nocturnal basking: manual surveys

3.3.1. *Trachemys venusta* (Emydidae; Belize)

From 28-Jun-2020 to 1-Aug-2020 (inclusive), a small, shallow pond with multiple basking structures was manually searched via head torch between 19:00–19:30 h each night. One nocturnally basking individual was observed on the 28th and three were observed on the 31st. None were observed out of the water on other nights. Two individuals appeared wet, suggesting recent emergence, while the other two appeared largely dry. A trail camera trap was deployed on a basking log in the pond from 22-Jul-2021 to 28-Jul-2021. A large rainfall event on 23-Jul-2021 raised the water levels and submerged many of the basking structures. No individuals were documented basking nocturnally via the camera trap, but 53 diurnal basking events were recorded. This pond contained several small, resident Morelet's crocodiles (*Crocodylus moreletii*) and numerous potential predators were in the area, including multiple heron species and large mammals such as jaguars (*Panthera onca*).

Table 3

Survey results for *Nilssonina* (Trionychidae) and *Pangshura* (Geoemydidae) species at three temple ponds in India over two seasons (summer | autumn). Ponds = number of ponds where a species was detected, Surveys = number of surveys (out of 21 [3 ponds and 7 surveys per pond]) where a species was detected, Count = number of basking observations (sum of individuals across surveys).

	Species	Summer Autumn		
		Ponds	Surveys	Count
Diurnal	<i>N. gangetica</i>	3 3	16 17	24 30
	<i>N. hurum</i>	3 3	14 6	22 7
	<i>N. nigricans</i>	3 3	20 14	36 26
	<i>P. smithii</i>	2 1	2 1	2 1
	<i>P. sylhetensis</i>	3 3	6 5	7 7
	<i>P. tecta</i>	3 3	12 11	18 15
	<i>P. tentoria</i>	3 2	5 2	6 3
Nocturnal	<i>N. gangetica</i>	0 0	0 0	0 0
	<i>N. hurum</i>	0 0	0 0	0 0
	<i>N. nigricans</i>	2 0	5 0	5 0
	<i>P. smithii</i>	1 0	2 0	2 0
	<i>P. sylhetensis</i>	3 2	8 4	9 4
	<i>P. tecta</i>	3 0	7 0	9 0
	<i>P. tentoria</i>	3 2	5 2	6 2

3.3.2. *Nilssonia* spp. and *Pangshura* spp. (Trionychidae and Geoemydidae; India)

In summer (May) and autumn (October), three large, outdoor temple ponds (each 4675 m²) were manually searched for basking turtles. In each season, each pond was searched seven times during the day (between 10:00–11:50) and seven times during the night (between 22:40–23:50). Air temperature was recorded during each survey. Seven species (three *Nilssonia* spp. and four *Pangshura* spp.) were observed basking during the day, and five species were observed basking at night (Table 3). All nocturnally basking species were observed at least twice. There was a significant negative relationship between air temperature during the survey and the number of nocturnally basking turtles observed (based on a linear mixed effects model with temple pond included as a random effect; $\chi^2 = 28.6$, df = 1, $P < 0.0001$). Air temperatures during the surveys were cooler in summer than in autumn, and most nocturnal basking events took place in summer (Fig. 7). Previous work in Indian temple ponds also documented nocturnal basking in *N. gangetica* and *N. hurum* (Barhadiya et al., 2020), but they were not observed basking at night in the present study (note that *N. gangetica* and *N. hurum* were not scored as nocturnal baskers in our previous analyses comparing the latitude of species that did and did not bask at night in this study; however, scoring them as nocturnal baskers did not alter the result: $\chi^2 = 5.03$, df = 1, $P = 0.0249$). The temple ponds supported predatory catfish (*Clarias gariepinus*) and large *Nilssonia* spp. which can eat small turtles.

3.4. Nocturnal basking: anecdotal observations

3.4.1. *Kinosternon scorpioides* (Kinosternidae; Trinidad and Tobago)

At ~20:00 h on 20-Aug-2021, an adult *K. scorpioides* was observed basking on a concrete drain ~15 cm from the water. There was a visible trail of water from the drain to the turtle's body. The turtle was observed for ~30 min at interspersed distances between 30 cm and 3 m. The turtle stayed at the exact same location and did not exhibit any other behavioural traits. At ~20:30 h, the turtle turned around, crawled back to the water, and swam away. Water in the drain had a relatively high flow rate but was shallow at the time (~5 cm deep and 30 cm wide). The concrete drain, which was gently sloped, ran parallel to residential homes on the street to the north and the coastline to the south. There was a full moon with clear sky conditions during the night of the observation. No further nocturnal basking was observed during the subsequent 11 nights at the location (21-Aug-2021 to 30-Aug-2021). Potential predators were predominantly birds (e.g., herons).

3.4.2. *Elseya irwini* and *Myuchelys latisternum* (Chelidae; Australia)

In December 2020 at The Canopy Treehouses (Atherton Tablelands, Queensland) several turtles were observed basking on rocks at night (R. Pillai pers. comm. [James Cook University, oral communication, 2020]). Both *E. irwini* and *M. latisternum* are abundant at this site and the turtles were not identified to species. Trail camera traps were subsequently deployed (1021 h of deployment). It was generally not possible to differentiate the two species in the photographs due to morphological similarities and they are discussed together (*E. irwini*/*M. latisternum*) unless otherwise noted; however, both species were confirmed in at least some photographs.

Only one emergence (*M. latisternum*) was documented after dark (duration = 2 min). An additional turtle (species unclear) emerged onto a tall rock (~1.5 m above the water) far from the camera at 16:06 and remained there until at least 18:58. The sun set at 18:43 and the camera entered its "night" (infrared flash) mode at 18:48. Because of the distance from the camera, it was not possible to see the turtle after 18:58, and it is not clear for how long it stayed out. There were few potential turtle predators at this site (mostly birds).

Camera traps were also deployed at a second site (Burbengary, Queensland) with *M. latisternum* (1874 h of deployment), but only one *M. latisternum* was observed basking, and it was during the day. It is also worth noting that from 2015 to 2018, one author (DTM) conducted numerous frog spotlighting surveys along lengthy sections of rainforest creeks containing *M. latisternum* (see maps in McKnight et al., 2020, 2017) and never observed *M. latisternum* basking at night but did frequently see them in the water at night or basking during the day.

3.4.3. *Elseya lavarackorum* (Chelidae; Australia)

On 17-Nov-2021, while canoeing at Boojamulla (Lawn Hill) National Park at night (20:00–23:00 h), two turtles were observed basking nocturnally: one on a piece of wood floating downstream, and one on a log next to shore. The former dove back into the water

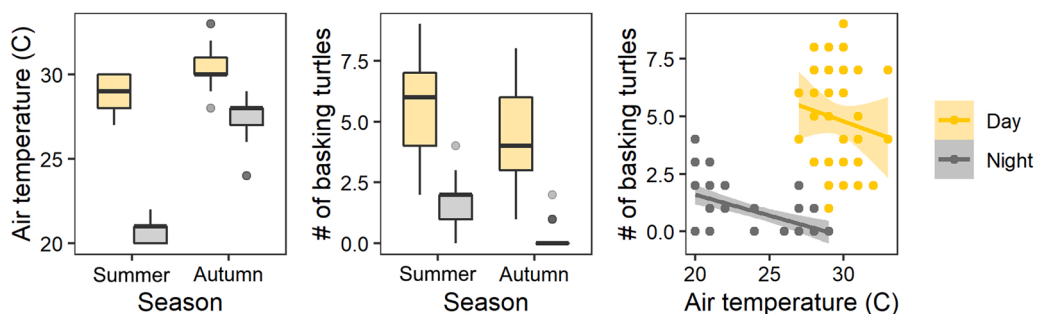


Fig. 7. Temperatures (A) and number of basking individuals per survey (B) for *Nilssonia* spp. (Trionychidae) and *Pangshura* spp. (Geoemydidae) in India (all species combined per survey). C = Number of individuals per survey regressed on air temperature. Boxplots were made using the default formula in gplot2 (v3.3.6). Shaded areas on the scatter plot indicate 95% confidence intervals.

before the species could be identified, but the latter was confirmed as *E. lavarackorum*. This species was previously observed basking at night on rocks beside small waterfalls at this site (Cann and Sadlier, 2017; Schaffer pers. com. [James Cook University, oral communication, 2020]). This site contained numerous *C. johnstoni* and predatory birds.

3.4.4. *Pelusios castanoides* (Pelomedusidae; Seychelles)

From 2005–2011, wild-caught *Pelusios castanoides* and *Pelusios subniger* were kept at a breeding facility on Silhouette Island. They were maintained in large outdoor enclosures (~2.16 m²) with ~1.35 m² ponds. Adult (but not juvenile) *P. castanoides* were frequently observed emerging at night, with at least some individuals emerging on most nights. Some emergences were short, but others lasted over an hour. *Pelusios subniger*, in contrast, was never seen emerging at night. In these captive ponds, *P. castanoides* frequently had algal growth on their shells (rarely observed in the wild), raising the possibility that nocturnal basking was a means of drying the shell and could be an artefact of captivity. *Pelusios subniger* did not have algal growth, possibly because they spent several months buried on land (a behaviour in which *P. castanoides* did not engage). These observations were provided by J. Gerlach (pers. comm. [University of Cambridge, written communication, 2022]).

3.5. Diurnal basking

Durations of diurnal basking events were generally short (median = 18 min, range = 2–601 min, N = 7191), with 37.5% of events lasting ≤ 10 min, 46.1% ≤ 15 min, and 55.8% ≤ 20 min (based on all data from all species/sites/seasons regardless of sample size; Fig. 6). Somewhat similar results were obtained after controlling for differences in sample sizes by examining the medians for species/sites/seasons with ≥ 30 data points: 11.1% of median durations were ≤ 10 min, 33.3% were ≤ 15 min, and 48.1% were ≤ 20 min. There were, however, a few very long diurnal basking events, the longest of which lasted 10 h (*Trachemys scripta*, summer, Arkansas USA). There was a significant trend of increasing mean duration of basking events with increasing distance from the equator ($\chi^2 = 4.6003$, df = 1, P = 0.0320).

Diurnal basking activity of freshwater turtle species generally started ~3 h before midday, peaked near midday, and gradually declined until sunset (Figs. 2 and S1). The peak was around midday or late morning across a wide range of latitudes (Fig. 2), and there was not a significant relationship between the timing of peak basking activity and distance from the equator ($\chi^2 = 0.177$, df = 1, P = 0.674). There was, however, a significant negative relationship between distance from the equator and the percent of basking activity (minutes of basking) that occurred during the hour of peak basking activity ($\chi^2 = 5.576$, df = 1, P = 0.018). Thus, basking activity was less concentrated in a peak period further from the equator.

Our ability to examine broad seasonal patterns was limited because of uneven sampling of freshwater turtle species across sites and seasons; however, there appeared to be a general pattern of basking shifting later in the day in the summer than spring (Fig. S1). There were six cases where a species/site had ≥ 30 data points in more than one season, and they showed considerable seasonal variation in diurnal basking activity (Fig. 2). For a wild population of *Emys orbicularis* in Germany, spring basking was shifted strongly to the morning, whereas summer basking was shifted strongly to the afternoon (W = 36.498, P < 0.0001). *Chrysemys picta* in Ohio (USA) also basked primarily in the morning in spring, with a less pronounced morning peak in summer, and a peak closer to midday in autumn (W = 29.571, P < 0.0001), but this difference was less obvious than it was for *E. orbicularis*. All post hoc pairwise comparisons between the three seasons were significant for *C. picta* (all P < 0.02 after applying a sequential Bonferroni correction). *Trachemys scripta* in Arkansas (USA) similarly shifted to basking later in the day in autumn compared to summer (W = 16.061, P = 0.0003), while *T. scripta* in Trinidad and Tobago basked primarily in the morning in both October and December, with a stronger morning shift in October than December (W = 21.229, P < 0.0001; both sampling periods were within the rainy season). *Myuchelys bellii* in New South Wales (Australia) basked predominantly at midday in the spring, with a more spread-out distribution in the summer (W = 7.366, P = 0.0252). Arguably the strongest seasonal shift occurred for *E. macquarii* in Townsville (Australia; W = 227.02, P < 0.0001). This was driven largely by an abundance of nocturnal basking in summer, however, even if the comparison was restricted to diurnal basking events, the winter months showed a stronger peak in mid-afternoon than did the summer months (W = 80.912, P < 0.0001).

4. Discussion

4.1. Nocturnal basking

We documented nocturnal basking in a wide range of freshwater turtle species (six families, including both suborders: Pleurodira and Cryptodira; Fig. S2) and longitudes, occurring in Central America, Trinidad and Tobago, the Seychelles, Africa, Asia, and Australia. Before this work, nocturnal basking was only known from a few scattered, anecdotal reports (Cann and Sadlier, 2017; Barhadiya et al., 2020; Nordberg and McKnight, 2020). This is the first study to document a widespread occurrence of this behaviour, and our results suggest that nocturnal basking may be a common and almost entirely overlooked aspect of many species' ecology.

We found a clear latitudinal pattern in nocturnal basking behaviour. All nocturnal basking activity was confined to populations in the tropics and a few sub-tropical locations just outside the tropic zone. This suggests that the behaviour is at least partially related to environmental temperature and is driven by the higher temperatures at lower latitudes. Indeed, for *E. macquarii* in Townsville, Australia (the site with the highest level of documented nocturnal basking), there was a positive relationship with environmental temperature, with substantially more nocturnal basking activity (both in frequency and duration) in summer than in winter. Further, a longer-duration survey of this population found that both *E. macquarii* and freshwater crocodiles (*C. johnstoni*) increased nocturnal basking frequency when the water temperature was simultaneously high and higher than the air temperature (Nordberg and

McKnight, in press). Likewise, a lab-based experimental study of Townsville *E. macquarii* found that turtles were more likely to bask nocturnally when exposed to a high water temperature (29 °C; a common temperature in the Ross River) while the air temperature was at their thermal preference (26 °C; Kidman et al., in press). Taken together, these results suggest that, at least for some tropical populations, nocturnal basking can be a mechanism for thermoregulatory cooling. Research on reptile thermoregulation has often focused on diurnal activities because of solar radiation, but recent work has shown that some tropical snakes and lizards behaviourally thermoregulate at night (Anderson et al., 2005; Nordberg and Schwarzkopf, 2019). Likewise, on particularly warm nights, *C. picta* in North America have been observed sitting at the surface of the water with their head or top of their shell exposed (J. Iverson pers. comm. [Earlham College, written communication, 2022]). Interestingly, Hjort Toms et al. (2022) found that nocturnal emergence and terrestrial movements of Spotted Turtles (*Clemmys guttata*) were not thermoregulatory; however, that work was conducted in Ontario, Canada, where nocturnal emergence would likely expose turtles to sub-optimal temperatures (as the authors documented). Additionally, the turtles in Hjort Toms et al. (2022) walked around on land (up to several hundred meters), rather than remaining stationary and “basking” as the turtles in our study did, suggesting that a different behaviour was occurring.

In contrast to *E. macquarii* in Townsville, turtles in India exhibited more nocturnal basking on cooler nights, rather than warmer nights, and *P. adansonii* in Africa spent more time basking nocturnally in winter than in summer. The reasons for these differences are unclear. It may be that at some sites or seasons, turtles are escaping unfavourably warm water temperatures, while at others, they are taking advantage of the warm tropical air to increase their body temperature and escape unfavourably cold water. Alternatively, at some locations, nocturnal basking may not be directly for the purpose of thermoregulation, but the higher night-time temperatures in the tropics may allow turtles to emerge for other purposes, such as predator avoidance (Barhadiya et al., 2020; Nordberg and McKnight, 2020).

Previous observations of *Nilssonina* spp. and *Pangshura* spp. basking at night were limited to small individuals, suggesting the avoidance of predators (e.g., large turtles) that would not be a threat to adults (Barhadiya et al., 2020). In the present study, most *Nilssonina* spp. and *Pangshura* spp. were juveniles, but several larger individuals were observed basking nocturnally, and for all other species, nocturnal basking observations included adults. Further, *E. macquarii* from Townsville (Australia) cohabitate with dense populations of freshwater crocodiles (five *C. johnstoni* per km of river; Nordberg and McKnight in press), and turtles were often seen basking with or on top of crocodiles during the day (Fig. 4), suggesting predator avoidance is unlikely to be the primary factor driving nocturnal basking. Additionally, nocturnal basking was also observed at locations that lacked aquatic predators of adult turtles (e.g., *P. adansonii* in captive ponds in Senegal, *E. irwinii*/*M. latisternum* in Australia, and *E. macquarii* in Brisbane, Australia) as well as locations where the behaviour likely increases their risk of predation from avian and mammalian predators (e.g., *T. venusta* in Belize and *K. scorpioides* in Trinidad and Tobago). It is possible that predator avoidance is a factor at some sites and not others (depending on the type of predators [e.g., terrestrial or aquatic], turtle densities, predator densities, and availability of basking structures), but it does not explain the behaviour across all sites.

Additionally, diurnal basking has been proposed to have many benefits beyond thermoregulation, such as shell maintenance (e.g., scute drying or to reduce algal growth) and skin desiccation to remove parasites (Ibáñez et al., 2014; Mcauliffe, 1977). Warm tropical climates may allow turtles to obtain some of these benefits during the night as well as during the day. However, it should be noted that McKnight et al. (2021) found that basking (either diurnal or nocturnal) was not effective for removing leeches from *E. macquarii*.

Interestingly, we did not find any evidence of nocturnal basking in North America, but Neill and Allen (1954) anecdotally noted seeing *Pseudemys* spp. emerge at night and assume a stereotypical basking posture, and Boyer (1965) noted that he had seen “similar examples” (in reference to Neill and Allen’s note). However, neither study noted the locations or seasons of these observations, the sizes of the turtles, or whether the turtles were in captivity. Many of the other observations in Neill and Allen (1954) were, however, from Florida (where both authors were based [not sampled in the present study]), which would be consistent with our result that nocturnal basking is restricted to more tropical climates.

We observed nocturnal basking across multiple turtle lineages, suggesting that the behaviour may be evolutionarily labile, with gains or losses not strongly constrained by phylogenetic history, at least at deeper levels of divergence (see phylogenetic tree: Fig. S2). Unfortunately, we were unable to properly test for a phylogenetic signal because phylogeny was highly confounded with geography. For example, only one Emydidae (*T. venusta*) basked at night, but most of the Emydidae data came from temperate climates. Similarly, Chelidae had high rates of nocturnal basking, but most of the Chelidae data came from tropical and sub-tropical portions of Australia. A more complete understanding of which species bask nocturnally is needed before proper phylogenetic analyses can be conducted, but the current evidence suggests that it is probably not phylogenetically constrained. This will be an interesting direction for future research.

It should also be acknowledged that our observations of *P. adansonii*, *P. castanoides*, *N. nigricans*, and *Pangshura* spp. came from captive populations. While those enclosures were large, outside, and likely fostered natural behaviours, it is, nonetheless, difficult to eliminate the possible influence of captivity, and it would be useful to look for nocturnal basking in wild populations of those species. Additionally, there was a statistically significant difference between the absolute values of the latitudes of diurnally and nocturnally basking species even after removing all captive populations.

Although many freshwater turtles appear to nocturnally bask at least occasionally, there was considerable variation in the frequency of the behaviour. *Trachemys venusta* and *E. irwinii*/*M. latisternum*, for example, were both occasionally observed basking at night, but subsequent camera deployments at the same locations and times of year failed to detect them. Likewise, at temple ponds in India, we observed nocturnal basking in three previously reported species (*N. nigricans*, *P. sylhetensis*, and *P. tentoria*), but we did not observe nocturnal basking in *N. gangetica* or *N. hurum* (which had been previously reported basking at night), and we observed nocturnal basking in *P. smithii* and *P. tecta* (which had not been previously reported basking at night; Barhadiya et al., 2020). Further, most temple pond species were observed basking nocturnally on only a few surveys (max = 8/21). Thus, while this behaviour is not

rare at these sites, it is also not particularly prevalent. In contrast, *E. macquarii* in Townsville appear to frequently bask nocturnally, particularly in the summer, with nocturnal basking events comprising 18.1% of all summer basking events. However, far fewer nocturnal basking events were observed further south for *E. macquarii* in Brisbane (4.4% of all basking events), but seasonality is also a likely factor. Interestingly, no nocturnal basking was observed for *E. macquarii* in Burpengary (just north of Brisbane) or in South Australia. Despite this variation, nocturnal basking events were consistently less frequent than diurnal basking across species and sites, though in some cases, the durations were considerably longer.

Animal personality traits, including boldness or propensity to bask are known to vary within populations (Caldwell et al., 2017; Refsnider et al., 2018). We were unable to monitor the individual identities of turtles throughout this study, but a more detailed study at locations where nocturnal basking is prevalent would provide valuable insight into how widespread nocturnal basking is within a population. Similarly, quantifying additional metrics about individuals that engage in nocturnal basking could identify trends related to body condition, mass, reproductive status, ectoparasite load, sex, or age class that may contribute to the propensity to emerge at night.

4.2. Diurnal basking

Although we were specifically looking for nocturnal basking, we simultaneously collected a large and valuable dataset on diurnal basking behaviour. Turtles are often observed basking in the early morning, just after sunrise, to increase body temperature (Peterman and Ryan, 2009; Schwarzkopf and Brooks, 1985; Selman and Qualls, 2011) or in the late afternoon before the sun sets (Peterman and Ryan, 2009; Selman and Qualls, 2011); however, we generally observed most diurnal basking at roughly the mid-point between sunrise and sunset or just before the midpoint (Clavijo-Baquet and Magnone, 2017; Crawford et al., 1983). Basking when the sun is directly overhead provides more direct solar radiation, minimising basking duration and allowing turtles to return to the water as quickly as possible to resume other activities (e.g., foraging and searching for mates; Angilletta, 2009). There was, however, variation among species and sites.

Many previous studies have found that basking patterns in turtles are affected by seasons (Clavijo-Baquet and Magnone, 2017; Coleman and Gutberlet, 2008; Hammond et al., 1988). Likewise, we found a general trend across species of a higher portion of basking activity occurring late in the afternoon in the summer compared with spring (Fig. S1). Similarly, temperate peak basking activity for *T. scripta* and *C. picta* occurred near midday in the spring and autumn but shifted to early morning in the summer. However, other species, such as *Emys orbicularis* followed different patterns, possibly due to latitudinal effects. There was also some evidence of longer mean basking durations further from the equator, as well as reduced concentration of peak basking activity. Our ability to assess these patterns was, however, limited, and these results should be viewed cautiously. Little work has been done on the effects of latitude on basking behaviour and this would be a valuable topic for future studies.

Finally, our data suggest that diurnal basking durations of freshwater turtles were fairly short (over 50% of basking events ≤ 20 min). This is an important consideration when discussing possible drivers of basking behaviour, because most basking events may be too short for functions such as drying skin and removing ectoparasites (McKnight et al., 2021). It is also possible that individuals bask for multiple reasons, and the duration of the event depends on the specific purpose at that time (e.g., individuals with infections may choose to bask for longer periods than would normally be necessary for thermoregulation) and may be interrupted by human activities (e.g., boating). As previous authors have noted, basking is likely a complex trait that is influenced by a myriad of factors (Hammond et al., 1988).

5. Conclusions, limitations, and future directions

Nocturnal basking has only recently been reported in wild turtles, but this study suggests that the behaviour is widespread and occurs in many families and species. Nevertheless, the behaviour appears to be restricted to tropical and sub-tropical regions, suggesting that it is largely influenced by environmental temperatures; however, additional factors may be at play at different locations and for different species. Our ability to make broad comparisons was inherently limited by seasonal differences in camera trap deployment and the fact that several records came from anecdotal observations or manual surveys that could not collect duration data, and more work is needed. It would be particularly informative to select several wide-ranging species or genera and conduct replicated basking surveys across their ranges, altitudes, seasons, and environmental factors (e.g., moon phase) to document basking activity. Trail cameras would provide an easy and inexpensive method for conducting these surveys.

This study is simply the first critical step in understanding this behaviour, and now that it has been widely documented, more focused research can be conducted to better understand the factors that influence it. These initial results suggest that nocturnal basking is likely an overlooked aspect of the ecology of many species and given that it appears to be influenced by environmental temperatures, it may also have implications for turtles' persistence and behavioural changes under climate change.

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CRediT authorship contribution statement

Eric J. Nordberg and Donald T. McKnight jointly designed the study, organized participants, and led the data analysis and writing. All authors contributed data, provided input, and edited the paper.

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.

Data availability

Partial data are available from the US Geological Survey (Glorioso, 2022) and a full data set is available on Dryad (<https://doi.org/10.5061/dryad.sj3tx968z>)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02444](https://doi.org/10.1016/j.gecco.2023.e02444).

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