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METHODOLOGY

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User- and budget-friendly accelerometers highlight vulnerability to poaching and weather extremes for a Critically Endangered turtle

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Abstract
Understanding how animals allocate their time and resources across the diel cycle and in response to environmental conditions is fundamental to ecology and conservation. While the use of accelerometers has enabled detailed descriptions of activity patterns and energetics of animals, its application to small- to medium-sized animals remains limited. This study describes a methodological approach for monitoring activity budgets in those instances using purpose-built accelerometry and hidden Markov models (HMMs). We demonstrate this approach by investigating the activity profile of five Critically Endangered big-headed turtles, *Platysternon megacephalum* (2 females and 3 males). Using a user- and budget-friendly tri-axial accelerometer designed for small- to medium-sized animals, we collected high-resolution data on the locomotory behaviors of *P. megacephalum*. We categorized the accelerometry data into two distinct behavioral states: (i) stationary and (ii) mobile using HMMs in an unsupervised setting. Our approach successfully quantified key locomotory-related behaviors in a cryptic species, revealing that individuals spend approximately 87% of their time stationary, with significant variations in activity related to sex, diel cycles, and weather conditions. Female turtles exhibited a crepuscular activity pattern, peaking at dawn (03:00–10:00) and dusk (17:00–20:00), while males demonstrated a more cathemeral profile (05:00–12:00). These results suggest that females and males could be unevenly targeted by poaching, with males being most susceptible to trap deployment. Notably, increased temperatures and precipitation positively correlated with increased activity levels within daily budgets, highlighting potential vulnerabilities to extreme weather events. This research presents an accessible pipeline that bridges biologging innovation and behavioral ecology, enabling targeted conservation strategies for small- to medium-sized animals by translating raw sensor data into actionable ecological insights. This is exemplified in our study of *P. megacephalum*, where we underscore the importance of understanding intrinsic behavioral traits and their interactions with extrinsic threats in *P. megacephalum*, providing critical conservation insights aimed at mitigating their population decline.

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Background

Risk of population decline and extinction is dependent on both a species' sensitivity to environmental changes (intrinsic biological attributes) and the nature and extent of those changes (extrinsic threats) [1]. Understanding what extrinsic factors are driving population declines and why species are prone to extinction have been a primary focus in conservation biology. Previous and ongoing studies have identified links between human-induced environmental changes and biodiversity declines, such as land use change [2], overexploitation [3], climate change [4], and invasive species [5]. Intrinsic biological attributes – such as rarity [6], habitat specialization [7], trophic level [8], and body size [9] – have also been suggested to influence the vulnerability of species to various environmental stressors. Yet, in addition to the "what" and "why" questions, there are few studies exploring "how" drivers of extinction work, i.e., how animal's intrinsic biological attributes may inadvertently expose it to an environmental stressor.

Species of Chelonians exemplify this challenge. Trafficked in large volumes – accounting for 38% of total seizures of live animals recorded from the TRAFFIC Bulletin during 1996–2008 [10], many populations of turtles and tortoises are declining substantially in the wild due largely to overexploitation and ineffective regulation of wildlife trade [11, 12]. This demand for Chelonian species in wildlife trade as pets has been shown to be linked to consumers' preferences for rarity and certain desired morphological traits [12]. Preferences for certain habitats in Chelonian species also predispose them to higher capture rates by poachers [13, 14]. However, how the risk of poaching relates to the timing of animal activity remains relatively unexplored.

Anthropogenic climate change is also impacting many species, including Chelonians through increased storms, floodings, extreme temperatures, droughts, and rising sea levels. These weather conditions exert indirect influences on Chelonians by disrupting habitat suitability [15, 16], interfering with sex determination mechanisms [17], and increasing incidences of infectious diseases [18]. However, the direct impacts of these varying weather scenarios on the locomotion and energetics of Chelonians remain largely unexplored. Stochastic disturbances, such as heightened temperatures and rainfall events, can impact the energetics [19, 20], locomotor performance [21, 22], and sensory perceptions [23] of flying animals, with downstream consequences on their foraging success [24, 25]. However, there remains limited mechanistic understanding of how freshwater turtles and other aquatic animals respond to such stochastic events [26]. For instance, it remains unclear whether they present behavioral strategies during storms, such as seeking shelter or relocating to more stable environments. Insights into how animals cope under the influences of different weather scenarios are crucial for predicting ecosystem-level responses to future climatic change scenarios [27].

Activity patterns in animals are influenced by a complex interplay of biological [28], social [29], and environmental factors [30, 31]. Since animal activity mediates interactions between individuals and their environment, animals may alter their behaviors based on the conditions they experience [32]. This adaptability is also influenced by factors such as behavioral plasticity [33], environmental tolerance [34], and trophic position [35]. The capacity to adjust behaviorally – including through changes in activity patterns – to new conditions is therefore a key determinant of the immediate fate of the animals in human-modified landscapes; for example, animals have been demonstrated to adjust their activity when conditions turn unfavorable [31, 36]. Yet, such changes in daily rhythms can also have profound implications for their survival and reproduction [37].

Despite the importance of high-resolution activity patterns, field studies examining diel activity in animals remain rather limited, primarily due to challenges like observer effects [38], the elusive nature of monitoring animals [39], and the limited availability of sampling units [39]. Recent advances in biologging technology have revolutionized the field by enabling remote collection of uninterrupted behavioral data over extended periods [40, 41]. Tri-axial accelerometers, in particular, have allowed the collection of multi-dimensional data on animal movement at increasing temporal resolution, transforming the way in which key questions surrounding movement ecology are answered [42]. For example, accelerometers have been employed to study activity patterns in animals and to delineate circadian rhythms into various behavioral states [43]. Motion metrics derived from accelerometer logging have also been demonstrated to be a proxy for energy expenditures [44], which is associated with individual fitness [45]. The observable behavioral changes enabled through acceleration logging and other biologging methods facilitate a mechanistic understanding of how environmental variations influence animal fates, with possible ramification for their management and conservation, especially for at-risk species under the face of global change [46]. However, due to weight limitations, accelerometry research on small- and medium-sized animals (≤ 1 kg) thus far has been relatively limited [47].

In this study, we developed a tri-axial accelerometer that is adaptive and cost effective to systems involving small- to medium-sized animals with amphibious life-styles in rugged terrains (e.g., rocky streams). The low cost, low power, light weight and configurable accelerometer developed through this study overcomes a key barrier to improve our ecological understanding for one of the most threatened taxa on Earth – the Chelonians. To date, complete behavioral representations of activity in freshwater turtles have only been profiled for few species, including the painted turtle (*Chrysemys picta*) [48, 49], the Blanding's turtle (*Emydoidea blandingii*) [48, 49], the European pond turtle (*Emys orbicularis*) [50, 51], and the northern map turtle (*Graptemys geographica*) [52]. These study systems involved only freshwater species inhabiting slow flowing lentic systems and lack representation of animals from the Global South where heavy poaching pressure persists. Through the application of the developed accelerometer on an Asian stream-dwelling freshwater turtle species – the Critically Endangered big-headed turtle (*Platysternon megacephalum*) – we demonstrated how accelerometry can be applied in the studies of lesser-known Chelonian species and investigated how individuals of *P. megacephalum* allocated their energy across their diel cycles. Specifically, we categorized accelerometry data of *P. megacephalum* into two behavioral states – (i) stationary and (ii) mobile behaviors – using hidden Markov models (HMMs). We explored how activity of *P. megacephalum* vary (1) with sex, (2) along the diel cycle, and (3) across different weather scenarios with reference to changes in temperature and precipitation rate.

Methods

Study species

Platysternon megacephalum is distributed in southern China, Cambodia, Laos, Myanmar, Thailand, and Vietnam. The species inhabits fast flowing rocky streams [53] with preferences for wider and deeper pool system [14]. Dietary analysis suggests that the species primarily preys on fruits, plant matter, insects, crabs and mollusks with key ecological functions through facilitation of seed dispersal and germination [54]. However, due to drastic population declines primarily as a result of severe poaching pressure [55, 56], *P. megacephalum* has become extremely rare across its native range and is currently listed as Critically Endangered on the IUCN Red List [57]. The need for comprehensive studies on how different environmental stressors impact the survival of *P. megacephalum* is thus urgent to inform strategies aimed at preserving this critically endangered species.

Study systems

This study was conducted in a rocky stream in Kadoorie Farm and Botanic Garden, a private nature reserve in Hong Kong Special Administrative Region (22°09'–22°37'N, 113°50'–114°30'E). Elevation of the study site ranges 300–800 m above sea level. The study stream is characterized by fast flowing water and rocky substratum. Riparian vegetation primarily consists of secondary forest species and is dominated by *Machilus spp.* As the site is frequently patrolled and fenced from unauthorized entry, harvesting pressure and other anthropogenic disturbances are low compared to other streams in Hong Kong [56].

Turtle sampling

During wet seasons (Apr – Oct) across three consecutive years between 2020 and 2022, *P. megacephalum* were captured by setting baited hoop traps following the procedures described in Sung et al. [56]. Basic morphological data were collected upon capture of turtles. These included the measurement of straight-line carapace length (CL) and plastron length (PL) with the use of caliper; measurement of body mass using an electronic scale; and determination of sex by visual examination of secondary sexual characteristics. For the purpose of individual identification, all captured turtles were marked by marginal scale notching in a numbering system developed by Cagle [58], with adult turtles implanted with a PIT tag through an incision around the thigh.

Accelerometer design

To enable effective collection of acceleration data in small- to medium-sized animals like *P. megacephalum*, we developed a low-cost, low-power, light weight, and fully customizable accelerometer using the TinyDuino Platform (TinyCircuits, USA). The device comprises four hardware components: (1) an Arduino-compatible microcontroller equipped with an Atmel SAMD21 processor board and a Bosch BMA250 accelerometer chip (ASM2021-R-A [1.40 g]; TinyCircuits, USA), (2) a micro-SD card reader (ASD2201-R [1.36 g]; TinyCircuits, USA), (3) a lithium polymer battery (ASR00007 [290 mAh, 5.90 g], ASR00035 [500 mAh, 9.30 g]; TinyCircuits, USA), and a (4) micro-SD card (32GB SanDisk Ultra microSDXC UHS-I card [0.26 g]; SanDisk, USA) (Fig. 1A), with a total unit cost of approximately USD 50.

With a compact size of 20 mm x 20 mm x 8 mm (excluding the case) and a net weight between 8 and 13 g (excluding the case), the accelerometer can be deployed on animals weighting over 160 g, following the common 5% rule, with the allowable mass varying by the choice of battery and attachment method. This covers many freshwater turtle species, including *P. megacephalum*, whose body mass when sexually mature averages slightly

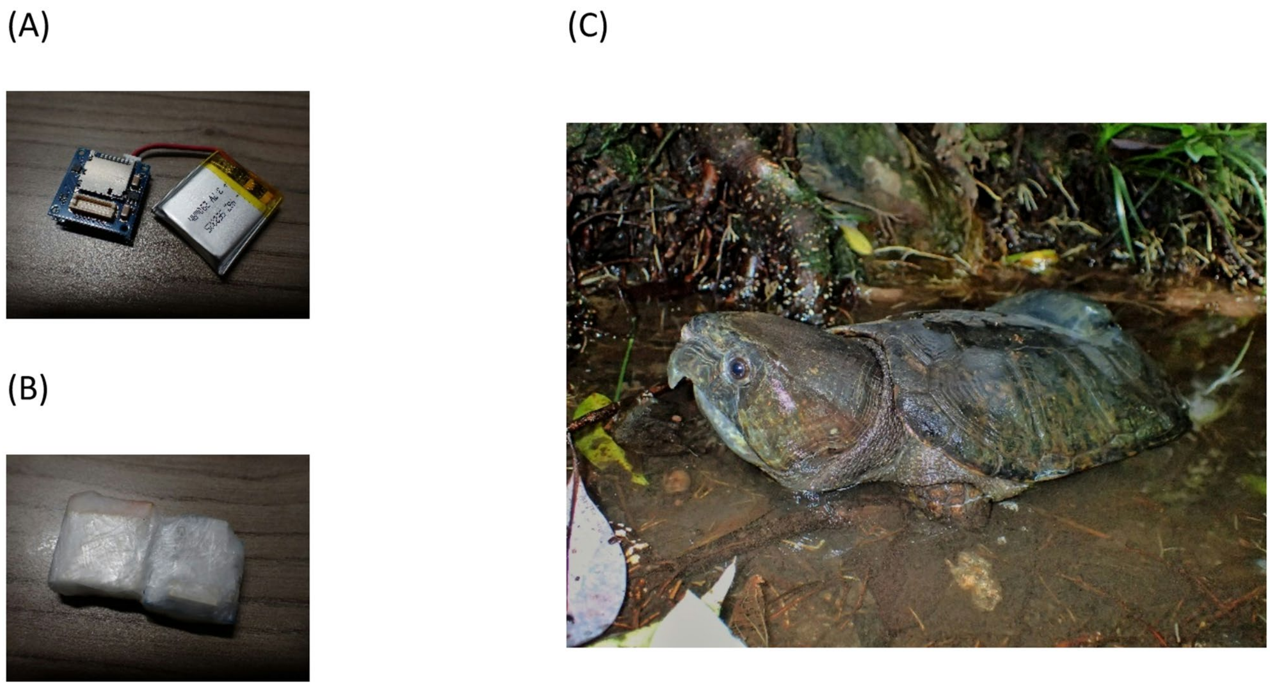

Fig. 1 Images of **A** the accelerometer unit, **B** the accelerometer unit packaged within layers containing zip-lock bags and Parafilm, and **C** individual *P. megacephalum* affixed with the accelerometer unit via epoxy putty glue

lower than 300 g (range: 180–1,180 g) in the study stream (Sung, unpublished data). Depending on an individual's body mass, we selected different batteries – the heavier battery offers a longer operational life (~ 23 days), while the lighter one offers a shorter life (~ 13 days). Accordingly, we applied casing materials of varying thickness, i.e., weight (10–30 g) to enclose the device, allowing for customization to remain within the allowed weight constraint. As a result, the total device weight (21–48 g, including radio transmitter) varied depending on the battery and the amount of casing materials applied.

The TinyDuino Platform's versatility enables user-defined parameters for encoding the operation of the acceleration transducer, allowing for continuous collection of acceleration profiles across multiple diel cycles even when battery capacity is limited by the animal's body mass. In this study, in order to comprehensively capture the activity profiles of *P. megacephalum*, we programmed the accelerometer to collect data at 15 Hz using a stratified sampling scheme that sampled for 15 s during each 15-minute interval. This method permits continuous data collection for about 2–3 weeks (cf. less than a day of operation using a non-stratified sampling approach). We selected a sampling rate of 15 Hz as it is the lowest supported by the software version of the TinyZero accelerometer board. This rate adequately meets our needs for distinguishing between stationary and mobile states [48]. To mitigate the influence of tagging and handling on the behaviors sampled, we programed an initial sleep period of 10 days, during which no acceleration data were recorded.

Functional verification of the developed accelerometer was performed to confirm its reliability in detecting movement onset and cessation. All materials and instruction necessary for building the device are available as open-source resources on the author's GitHub page (https://github.com/wingsingChan/PLME_Accelerometry_Public). It is important to note that this study did not include validation against a pre-existing reference device, as our objective was binary behavioral classification. For future studies of fine-scale behavioral classification, however, validation against benchmark devices is recommended to ensure measurement accuracy.

Accelerometer data collection

During the study period, 15 individuals of *P. megacephalum* (8 adult females and 7 adult males) were fitted with the tri-axial accelerometer. This included a total of 26 accelerometers independently deployed across 5 non-overlapping periods during the wet seasons (Table S1). Each unit was equipped with a radio-transmitter (SOPR-2190; Wildlife Materials International, Inc., New York, USA) to aid in retrieval. To protect the accelerometer from water damage, the device was sealed inside a zip-lock bag (95 × 49 mm) and tightly concealed with Parafilm sheets (Fig. 1B) before affixing onto the posterior margin of the turtle's carapace using epoxy putty glue (Fig. 1C). The total weight of the accelerometer unit

(20–48 g) – including the core electronics (8–13 g), the radio-transmitter (5–6 g) and the casing materials (10–30 g) – was kept under 10% (mean ± SD: 5.03% ± 1.02%, Table S2) of the turtle's body weight [60].

At the end of the study, 13 of the tagged animals were recaptured either through radiotelemetry or baited hoop traps, and 22 tags were retrieved for subsequent analysis (2 tags became detached from the recaptured individuals and were not recovered, and 2 tags went unaccounted for due to individuals missing from surveys). Attributing to hardware damage inflicted by the turtle's vigorous movements through confined spaces ($n = 8$) and incompatibility issues arising from library updates during the second deployment ($n = 6$), there was a high rate of premature failures to the accelerometers. Ultimately, only 8 functional accelerometers yielded sufficient data from the 5 sampled individuals (2 adult females and 3 adult males).

Quantifying environmental parameters

To evaluate the importance of environmental constraints on movement and behaviors of *P. megacephalum*, we collected temperature and precipitation data for the study area. Ambient air temperature and water temperature of the study stream were measured using two sets of temperature data loggers (iButton, MAXIM Integrated Product Ltd., USA) deployed at two different locales along the study stream. Each of the data loggers was housed within a PVC canister and secured within a mesh bag tied to a permanent structure. Temperature data were sampled at 15-minute intervals and were summarized based on the averaged values across the two sampling points.

Precipitation was assessed based on hourly data collected at a nearby weather station monitored by the Hong Kong Observatory. We further quantified heavy rainfall event at each individual time point whenever the rolling sum of the accumulated rainfall in the previous 24 h exceeded 30 mm, an amount comparable to the issuance of a rainstorm signal by the Hong Kong Observatory, albeit measured in a location-specific context.

Data processing

To quantify the activity profile and locomotory behaviors of *P. megacephalum*, raw acceleration data were aggregated into time series with equally spaced time intervals (1 s). Missing values (NAs) were added to maintain the continuity of the time series. Based on the tri-axial acceleration records, we then calculated the static component of acceleration by smoothing the raw accelerometer signal of each axis using a running mean of 15 s, a window length at which the ODBA began to stabilize [61, 62]. Dynamic body acceleration (DBA) was calculated by subtracting the raw acceleration measured at each axis from the static acceleration of the corresponding axis. To summarize individual locomotor movement, we calculated overall dynamic body acceleration (ODBA) based on the derived measures of DBA [61],

$$\mathrm{ODBA} = |\mathrm{DBA}_x| + |\mathrm{DBA}_y| + |\mathrm{DBA}_z|$$

Considering the temporal resolution of the acceleration data and the volume required for subsequent models, acceleration data were binned into 15-minute intervals based on aggregated means. Consecutive intervals with gaps greater than 15 min were split into individual tracks of uninterrupted sequences, and those with durations shorter than 24 h were filtered. To ensure the fitting of subsequent models, we included only individuals with accelerometry data totaling 72 h or more. This resulted in a total of 15 uninterrupted sequences (mean = 6.14 ± 2.95 days; max = 8.98 days) from across the 5 individuals (Table S3).

Data analysis

Through state-space modelling and regression analysis, we systematically assessed the behavioral states and time activity budgets of *P. megacephalum* based on accelerometry data collected from the 5 individuals. Specifically, hidden Markov models (HMMs) were used to segment and cluster the processed acceleration data into latent behavioral states. Using the magnitude of measured acceleration (i.e., ODBA), HMMs created cut-points (thresholds) that define behavioral states based on the intensity of physical activity. This framework provides a data-oriented approach to define behavioral states without requiring high quality labelled data [63, 64]. Following the classification of behavioral states, we investigated the temporal dynamics and environmental influences on activity through generalized additive models (GAMs). These models allowed exploration of activity patterns, as inferred from accelerometry-derived states, over time and in response to environmental conditions.

Hidden Markov models (HMMs)

An HMM is a state-space model that allows interpretation of the unobservable (hidden) state process by analyzing a sequence of observable events. At each time step ($T = 1, 2, \ldots, t$), the observable pattern ($Z_1, Z_2, \ldots, Z_t$) obtained from each data stream is assumed to be generated by N state-dependent probability distributions, i.e.,

$$\Pr(Z_t \mid Z_{t-1}, Z_{t-2}, \ldots, Z_1, S_t, S_{t-1}, \ldots, S_1) = \Pr(Z_t \mid S_t)$$

$Pr(Z_t \mid Z_{t-1}, Z_{t-2}, \ldots, Z_1, S_t, S_{t-1}, \ldots, S_1) = Pr(Z_t \mid S_t)$and the hidden state ($S_t \in \{1, 2, \ldots, N\}$) is assumed to follow a Markov chain, where the probability of the current state, S_{t+1} depends only on the previous state, S_t, i.e.,

$$\Pr(S_{t+1} \mid S_t, S_{t-1}, \ldots, S_1) = \Pr(S_{t+1} \mid S_t)$$

$\Pr(S_{t+1} \mid S_t, S_{t-1}, \ldots, S_1) = \Pr(S_{t+1} \mid S_t) Pr(S_{t+1} \mid S_t, S_{t-1}, \ldots, S_1) = Pr(S_{t+1} \mid S_t)$. The state sequence of the Markov chain is governed by the initial probabilities of the states, and the transition probabilities between states [66]. Within this context, the power of the HMM framework lies in its ability to capture the temporal dependencies and uncertainties inherent in real-world processes, making it widely utilized in the analysis of animal telemetry data over recent decades [67]. This includes classifying animal telemetry data into different latent behavioral states at different time steps [68].

Additionally, HMM allows the evaluation of covariate effects on state transition probabilities and on state-dependent probabilities [68]. This feature enables key insights into how environmental changes – such as photoperiod, temperature, and resource availability – impact state-dependent processes, i.e., the emergence of a behavior and transitions between behavioral states in animals.

We focused on classifying two general and biologically interpretable behavioral states in *P. megacephalum*: stationary (state 1), and mobile behaviors (state 2) using HMM. We assumed that periods of immobility (state 1) would be characterized by lower ODBA values, whereas periods of movement (state 2) would exhibit higher ODBA values. This binary classification was intended to capture major differences in activity intensity while minimizing uncertainty associated with more detailed behavioral categorization given limited understanding of Chelonian behaviors. A well-informed behavioral classification system based on accelerometry data is predominantly absent in freshwater turtles (except Auge et al. [48]).

To discern the two behavioral states, we employed the expectation maximization (EM) algorithm – an unsupervised machine learning method [69] – through the Rmixmod package [70]. Null individual-specific EM models were established based on the distribution of log-transformed ODBA measured for each individual, without considering temporal or environmental covariates. The mean and standard deviation of log-transformed ODBA from each EM-derived cluster were extracted to define the starting parameters for subsequent HMMs [71].

Following the specification of starting parameters, we fitted a series of 2-state HMMs for each individual using the momentuHMM package in R [68]. Individual-specific HMMs were fitted to ODBA using a log-normal distribution. To monitor how behaviors of *P. megacephalum* changed across the diel cycle, time of day (hour) was included as a covariate in the state transition probabilities. Although *P. megacephalum* is primarily considered a nocturnal species, individuals were also observed active outside nighttime hours. To capture this periodicity, we modelled the effect of hour as a temporal covariate using the cosinor function implemented in momentuHMM following a 24-hour cycle. We also considered that transition between states might be influenced by heavy rainfall, which was incorporated as a categorical fixed factor when modelling the state transition probabilities. To further elucidate whether temporal variations in ambient temperature and precipitation constrained the movement of individual *P. megacephalum*, we explored the effects of temperature and precipitation on the state-dependent distributions of ODBA.

To avoid the risk of convergence to local maxima, each individual-specific HMMs was fitted 100 times with different starting parameters. Initial values were randomly sampled from a uniform distribution parameterized using the state-specific means and standard deviations of log-transformed ODBAs derived via the EM algorithm. We selected the optimal model by maximizing the log-likelihood. Model fits were assessed using pseudo-residuals diagnostic plot via the plotPR() function implemented in the momentuHMM package, and validated through visual assessment of the resulting behavioral classification.

Generalized additive models (GAMs)

To test if the time activity budget of *P. megacephalum* changed over the circadian rhythm among individuals of different reproductive groups (females and males), we summarized behavioral states along individual tracks based on the behavioral classification established in each individual-specific HMM. The proportion of time spent in-mobile behaviors across the diel cycle was modelled as a function of hour via a cyclic cubic spline, with sex as a grouping parameter, using the generalized additive model (GAM) from the mgcv package [72] in R. We constrained the basis dimension (*k*) for the cyclic cubic spline to 3, enabling it to capture the diel periodicity while excluding high-frequency noise. We included sex and body weight as fixed effects, and individual ID, round of deployment and the nested effect of individual ID within round of deployment as random effects using the random effect smoother basis function in mgcv. For all other smooth terms, the optimal levels of smoothing were determined via Restricted Maximum Likelihood (REML).

The daily proportion of time spent in mobile behaviors by *P. megacephalum* was analyzed using GAM, with both daily average temperature and daily total precipitation modelled as fixed effects. We further included the sex-specific effect of Julian day via a penalized cubic regression spline function. Similarly, we included sex and body weight as fixed effect, along with individual ID, round of deployment and the nested effects as random effects. Basis dimensions for all smooth terms were determined by REML.

Both GAMs were fitted through a Tweedie distribution with a logit link function. Model selection was conducted to avoid overparameterization that may arise when fitting a complex model involved with nested random effects. For each instance, we compared the full model, which included the nested random effect, to an alternative model, where this effect was omitted using Akaike information criterion (AIC). The model with the lowest AIC value was chosen as the best-fitting model. The models omitting the nested random effect consistently had the lowest AIC and were selected as the most parsimonious model (Table S4). Model assumptions and outcomes were evaluated using the gam.check() function through mgcv package and DHARMa package [73] in R, respectively.

Results

State-dependent distribution of ODBA

Individual-specific HMMs developed based on a single data stream using ODBA effectively differentiated the activity levels of freshwater turtles into two distinct behavioral groups, which were identified as either (i) stationary or (ii) mobile state (Fig. S1). The ODBAs consistently discriminate between the two behavioral states across individuals of *P. megacephalum*, with an ensemble average of 0.0061 *g* (95% CI 0.0058–0.0065 *g*) for stationary behaviors and an ensemble average of 0.18 *g* (95% CI 0.12–0.26 *g*) for mobile behaviors (Fig. S2).

The effects of temperature and precipitation on the parameter of the state-dependent distributions were mostly inconclusive and varied among individuals of *P. megacephalum* (Fig. 2). Overall, the ensemble averages for the regression coefficient of temperature ($\widehat{\beta}$ = −0.20, $\widehat{\mathrm{SD}}$ = 0.42) and precipitation ($\widehat{\beta}$ = −0.34, $\widehat{\mathrm{SD}}$ = 0.64) suggested negligible influence. Despite the lack of unifying population-level responses, we observed individual differences in their responses to precipitation, with a male individual (ID471) demonstrating a slight increase in motion ($\beta = 0.085$, 95% CI 0.022–0.15), and a female individual (ID609) markedly reducing its motion (β = −1.47, 95% CI −0.96 – −1.98). Similarly, despite no net response to rising temperature on a population-level, a female individual (ID609) deviated from this pattern, with its activity declining significantly as conditions warmed (β= −0.93, 95% CI −0.47 – −0.93).

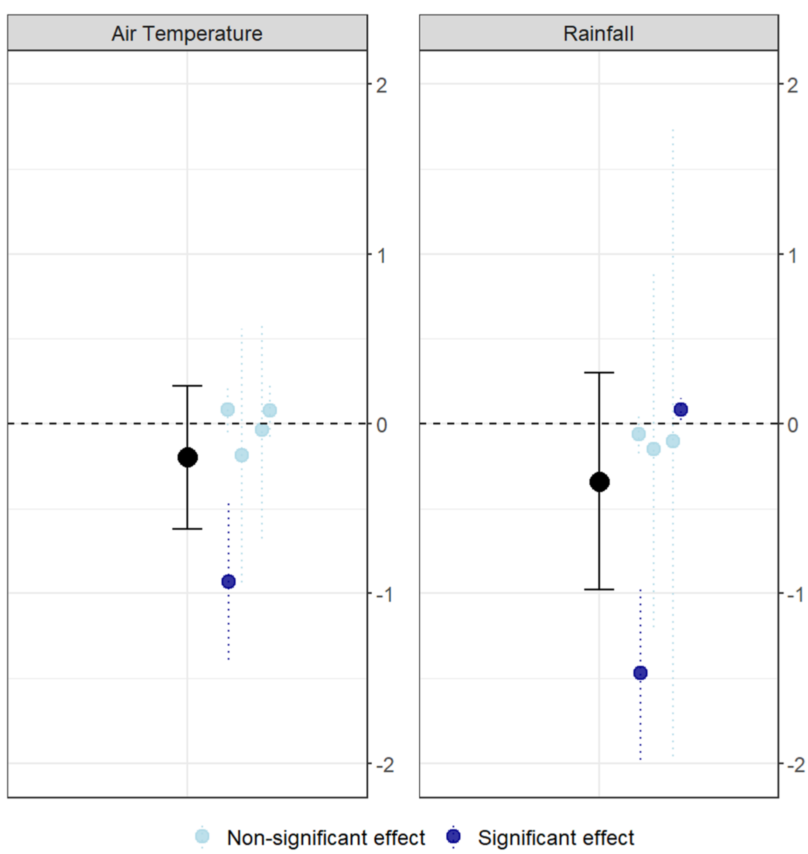

Fig. 2 Individual-specific coefficient values for the covariate effects of air temperature and precipitation on the state-dependent distribution of overall dynamic body acceleration (ODBA) estimated from hidden Markov models (HMMs). Ensemble averages and estimated averages are represented in black and blue dots respectively. Dark blue dots indicate significant effects. Error bars represent the 95% confidence interval

State-transition probabilities

The probability for transitioning from stationary to mobile behavior (0.065, 95% CI 0.042–0.10) was lower than that for transitioning from mobile to stationary behavior (0.46, 95% CI 0.29–0.62), indicating a greater barrier for becoming mobile.

Diel influence on transition probabilities varied among individuals, with most individual coefficient estimates overlapping zero (Fig. 3). In general, diel cycles identified through the cosinor function suggested that *P. megacephalum* remained mostly stationary throughout the daily cycle, with a slight increase in probabilities for transitioning to a mobile state at night and in the morning (Fig. S3). Most individuals in motion were more probable to remain active at night rather than being stationary (Fig. S3).

We recorded 5 heavy rain events, which included a total of 136 h of increased cumulative rainfall over the previous 24-hour periods. These events occurred during two accelerometer deployment phases across two individuals. Events of heavy rain substantially impacted the rate at which *P. megacephalum* transitioned between movement states (Fig. 3). Individuals were more likely to transition from a stationary to a mobile state during heavy rain ($\widehat{\beta}$ = 1.10, $\widehat{\mathrm{SD}}$ = 0.033). Similarly, the regression coefficient indicated that individuals in motion were less inclined to transition to a stationary state ($\widehat{\beta}$ = −0.86, $\widehat{\mathrm{SD}}$ = 0.27), i.e., they were more likely to remain mobile during heavy rain.

Time activity budget

By summarizing individual-specific HMMs, our results showed that *P. megacephalum* spent most of their time as stationary (86.80 ± 8.69%). The proportion of time spent being mobile varied consistently over the diel cycle and significantly differed between sexes (female: $F_{2,78}$ = 5.90, $P < 0.001$; male: $F_{2,60}$ = 22.27, $P < 0.001$). Female *P. megacephalum* exhibited a clear crepuscular activity pattern with a bimodal profile of activity that peaked around dawn and dusk (Fig. 4), whereas male *P. megacephalum* presented a cathemeral activity profile that was predominantly active at night and in the morning (Fig. 4).

Despite inconclusive evidence for the direct influences of environmental constraints on state-dependent

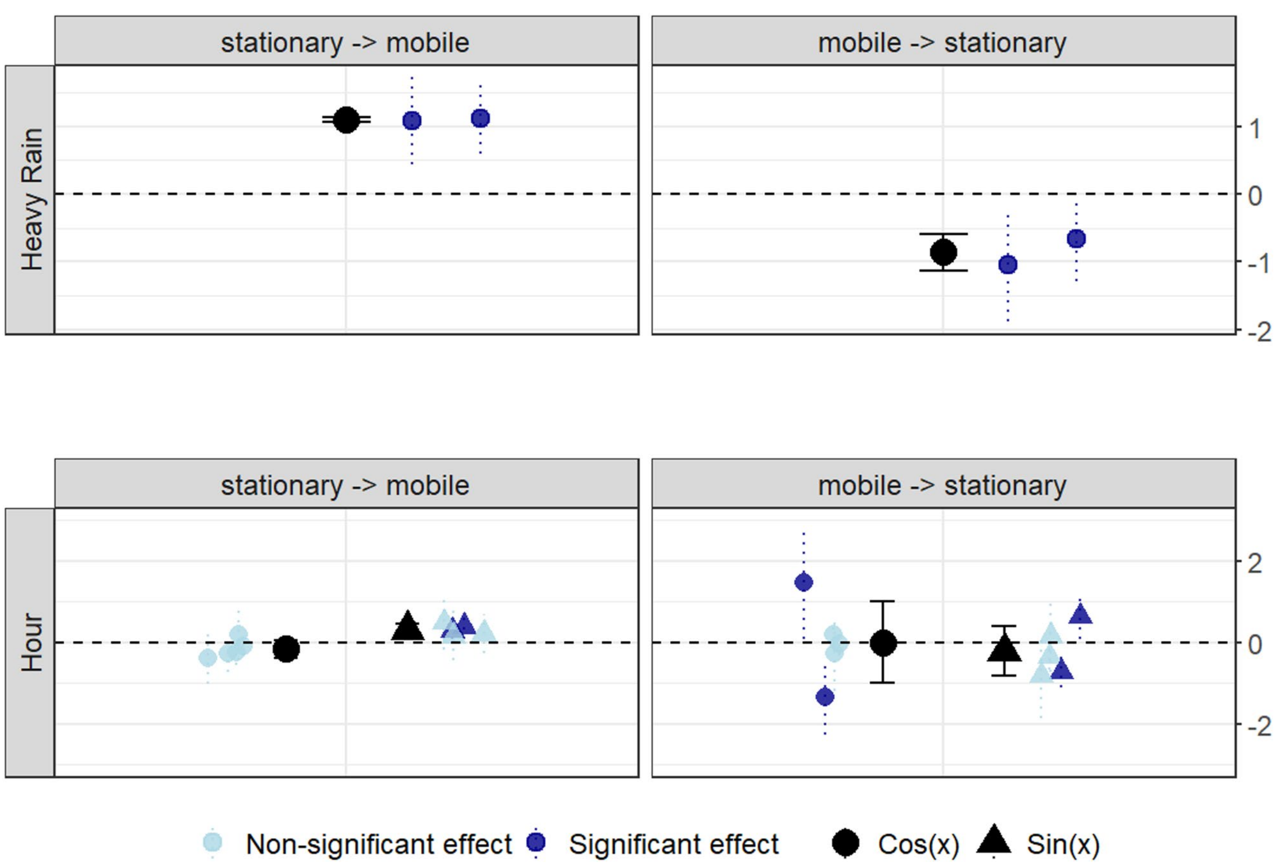

Fig. 3 Individual-specific coefficient values for the covariate effects of heavy rain and hour on state-transition probabilities between stationary (state 1) and mobile (state 2). Ensemble averages (black dots) and estimated averages (blue dots) were derived from individual-specific hidden Markov models (HMMs). Hour of day was fitted through a cosinor function, which included a cosine curve (●) and a sine curve (▲). Dark blue dots indicate significant effects. Error bars represent the 95% confidence interval

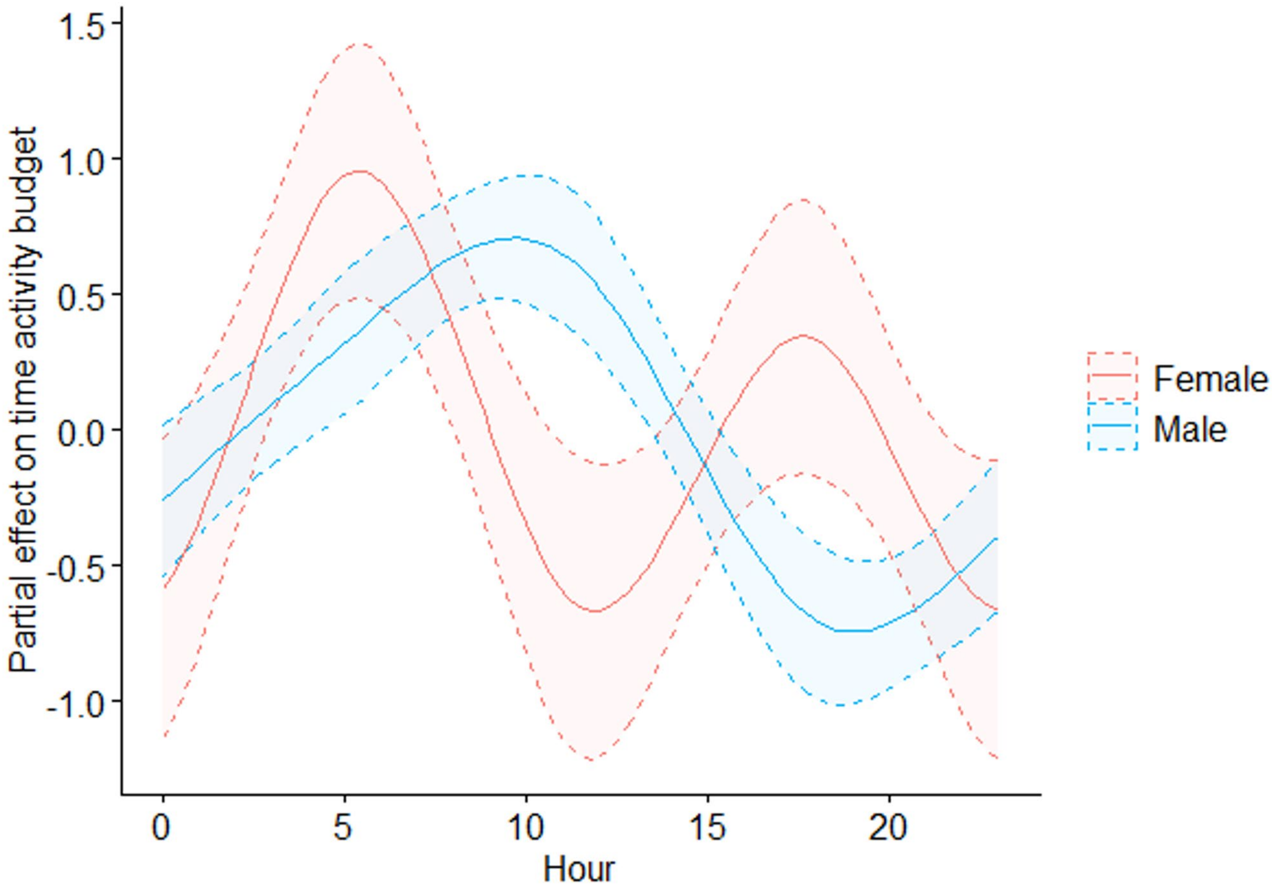

Fig. 4 Partial effect of hour modelled as a cosinor function following a 24-hour cycle on the time activity budget of big-headed turtles (*Platysternon megacephalum*) across different sexes: females (red) and males (blue). The dotted line represents the 95% confidence intervals (CI). Note that the 95% CI for female activity curves appear wider than for males, likely reflecting the smaller sample in females ($n=2$) than that in males ($n=3$)

parameter, time activity budgets of *P. megacephalum* increased with both increasing temperature (β = 0.37, odd-ratio = 1.44 [95% CI = 1.08–1.92], $t_1=2.50$, $P=0.014$, Fig. S4) and precipitation rates (β = 0.24, odd-ratio = 1.27 [95% CI = 1.03–1.56], $t_1=2.09$, $P=0.040$, Fig. S5).

Discussion

We provide a working demonstration of a custom-built accelerometer model suitable for measuring fine scale animal motion in small- to medium-sized animals. Following the application of this accelerometer model on a lesser-known species – *P. megacephalum*, we developed a species-specific behavioral classifier via an unsupervised HMM, which reliably delineates basic behavioral states across multiple individuals. This approach not only facilitates the characterization of the time activity budget in elusive animals, but also demonstrates how factors such as sex, temperature, and precipitation contribute to variations in the activity patterns of endangered species. This nuanced understanding about the activity patterns of *P. megacephalum* gives insight into how such behavior may influence their susceptibility to the dual pressures of overexploitation and climate change.

Advancing behavioral monitoring in lesser-known species

The methodological approach presented in this study highlights an advancement in monitoring the behaviors of freshwater turtles through innovative use of animal-borne accelerometers. By leveraging open-source tools, this research demonstrates the feasibility and a cost-effective approach of deploying the technology in small- to medium-sized animals, even in challenging environments characterized by prolonged underwater immersion and abrasive substrates. This approach not only mitigates the need for extensive field observations that could interfere with natural animal behaviors, but also opens new avenues for studying species that are typically difficult to observe at high resolution, thereby expanding the scope of behavioral research for endangered species.

Analytically, unlike supervised machine learning methods that require extensive labeled datasets, the unsupervised HMMs utilized in this study adeptly segment and cluster acceleration data to distinguish between key behavioral states through a cut-point based approach. The behavioral classifier established through this study demonstrates the utility of unsupervised methods in discriminating major behaviors in species that are understudied and hard to observe [64, 65]. For instance, uninterrupted observations of aquatic animals in their natural habitat are challenging. Meanwhile, recording observations in laboratory conditions away from their natural environment can induce abnormal behaviors (e.g., escape response, W. S. Chan, pers. obs.). However, we acknowledge that the unsupervised approach, while allowing for a non-a priori classification of broad behavioral types (e.g., stationary and mobile states), lacks the precision needed for fine-scale behavioral identification. There will be intermediate behaviors – such as slow movement, posture adjustment, and subtle sculling – that exist between the identified behavioral states. This may conflate specific activities (e.g., sit-and-wait foraging or thermoregulatory basking) within the mobile state. Validation studies, potentially using underwater video systems to provide video-referenced annotation while minimizing disturbance [74, 75], would be informative for future studies in refining the behavioral classifier [40].

Low activity budgets in *P. megacephalum*

We demonstrate that the activity budget in one of the most endangered freshwater turtle species is generally low. *Platysternon megacephalum* spends most of their time stationary, averaging less than 3 h of locomotor activity per day. This pattern of low activity observed through accelerometry aligns with the movement pattern observed in previous research using conventional telemetry technique, which reported modest weekly travelling distances for the species [14].

Comparatively, the low activity rate observed in *P. megacephalum* is similar to other freshwater turtle species, such as *E. blandingii* and *C. picta* (3.84 and 5.26 h, respectively [48]). The high levels of inactivity reported in these species may indicate a common strategy of energy conservation among freshwater turtles. The slightly lower activity rate in *P. megacephalum* relative to these species in a slow-flowing lentic system may reflect higher energetic costs associated with living in a fast-flowing lotic ecosystem. However, limited knowledge about freshwater turtle activity in the field prevents comprehensive assessments of habitat influence on energetics in freshwater turtles. Nonetheless, this result signals that energetic profiles of animals may be expressed differently across ecosystems [76]. We therefore encourage broader adoption of accelerometers within similar frameworks in research of freshwater turtles to enhance our understanding of the animals' energetic profiles across diverse ecosystems.

Activity profile of *P. megacephalum*

Platysternon megacephalum exhibits more diurnal and varied activity profiles than previously thought. Males are predominantly active early in the day (05:00–12:00), whereas females exhibit a more restricted activity window, with activity level peaks around twilights at dawn (03:00–10:00) and dusk (17:00–20:00). This pattern enabled through continuous acceleration data negates the common perception of nocturnality in *P. megacephalum* and corroborates anecdotal observation of *P. megacephalum* during non-nocturnal periods (W. S. Chan, pers. obs.).

The sex-specific activity patterns of *P. megacephalum* reveal a marked mismatch in the temporal activity between males and females, with females becoming active during dusk when males reduce their activity. This temporal partitioning may minimize intraspecific competition. Given the sexual differences in body sizes of *P. megacephalum*, females may temporally partition their resource use to avoid antagonistic encounters with larger males. While previous studies on the social behaviors of *P. megacephalum* found no significant differences in feeding sequences between sexes in captivity [77], the lack of differences may result from suppressed competition in controlled environments. Despite sex-specific differences, our study reveals a common activity window in the morning (05:00–10:00) shared by both sexes. By prioritizing foraging during hours before noon, individuals can maximize benefits gained from warmer temperatures by scheduling thermoregulatory and other temperature-dependent life essential processes, such as digestion and growth [78], in midday.

Vulnerability to poaching

Poaching of freshwater turtles, e.g., *P. megacephalum*, poses a significant challenge for conservation, largely due to a lack of detailed information about poaching activities. While seizure data and market surveys have illuminated the scale of the problem and identified species that are being targeted unevenly [11, 12], gaps in knowledge about how freshwater turtle species are being targeted by poachers hinder effective intervention to combat poaching. Through accelerometer-derived activity pattern, our study indicates that female *P. megacephalum* could be particularly vulnerable during twilight periods when they are most active. In contrast, the broader temporal niche and extended activity of males could increase their exposure to poaching activities. This sex-specific activity pattern in *P. megacephalum* suggests that females and males could be targeted unevenly, and male *P. megacephalum* may be most susceptible when poaching efforts are non-specific to the timing of day (e.g., long-term deployment of trapping apparatuses). Given the pronounced sexual size dimorphism (with males being larger) in *P. megacephalum*, the higher susceptibility of males to poaching may explain the smaller average body size observed in harvested populations of *P. megacephalum* [56]. Ultimately, the disrupted demography could have long-standing effects on the viability of the populations. Recognizing the unique needs and vulnerabilities of both sexes thus allows for tailored conservation efforts that enhance population resilience. Furthermore, our study suggests that early morning is a critical period during which both sexes of *P. megacephalum* are universally active. Therefore, prioritizing monitoring and patrolling efforts during this time in streams is essential for safeguarding the species.

Vulnerability to extreme weather scenarios

Despite their affinity to fast-flowing streams, our results indicate that *P. megacephalum* could still be susceptible to heavy rainfall at increasing intensity and frequency. Primarily, the state-transition probabilities suggest that *P. megacephalum* increased their activity levels (i.e., higher probability of switching into a mobile state) during heavy rainfall, rather than exhibiting stationary avoidance behaviors like refuge seeking. This increased mobility could be a direct consequence of forced displacement due to increased flow or turbulence. Alternatively, struggling behaviors to maintain position and other stress-induced movements might also contribute to increased motion. For instance, individuals might surface more frequently when inundated refuge limit opportunities for gaseous exchange, or when dive durations are reduced due to increased metabolic cost from navigating turbulent waters [79]. Observations of *P. megacephalum* on land are almost exclusively during or after heavy rains (Y. H. Sung, pers. obs.), suggesting that overland movement may be a strategy to evade increased flows in streams, contributing to increased mobility during heavy rain. While obtaining a definitive explanation for the increased mobility during heavy rain remains challenging without direct behavioral observations, exposure to heavy rainfall events at increasing intensity and frequency likely complicates an individual's energetic balance. This is well reflected by a positive change in the time activity budget of *P. megacephalum* as driven by increasing daily precipitation rates. Although previous studies investigating the influence of storms and hurricanes on the large-scale movements of various species of freshwater turtles suggested that such climatic events have minimal behavioral impacts [80–83], our findings from a fine scale locomotory perspective enabled through accelerometry indicate that even when the animal is not spatially displaced by extreme current, such events can alter the animal's behavioral response with downstream consequences on its energetic demand. This underscores the importance of having fine-scale behavioral understanding to assess their resilience amidst global changes [84].

Limitations and future directions

While the data presented in this study focused only on few individuals, the fine-scale depiction of activity profiles and locomotory behaviors in *P. megacephalum* is original with respect to data gathered through conventional biotelemetric methods or direct field observation. However, the small sample size and brief temporal window covered by the current study restrict broader ecological inferences. For instance, the current sample size limits the robustness of sex-specific inferences and their generalizability beyond the studied individuals. It should be noted with care that the reported differences in diel activity between sexes may be disproportionately swayed by the behaviors of single individual. Meanwhile, despite inconclusive population-level effects from the HMMs, the observed individual heterogeneity suggests individuals within the population may exhibit diverse behavioral strategies to environmental variation. While the temporal scope of this study limits our ability to robustly attribute these individual differences to specific causes or to predict their fitness consequences, such interindividual variation could be critical for understanding population resilience and individual vulnerability to environmental changes.

In addition, while the developed accelerometer model shows promise as a cost-effective alternative to remotely assess fine-scale behaviors in small- to medium-sized animals, several technical limitations warrant further consideration. First, the device's weight, while minimized, is primarily influenced by battery size, presenting a challenge for smaller animals. This constraint necessitates a stratified sampling design to conserve power. While this approach is justified on battery life performance, direct comparison between continuous and stratified sampling was not performed to quantify information loss. Additionally, infrequent data collection timeframes risk overlooking sporadic motions, future studies should explore adaptive programming that activates logging during movement and consider novel energy harvesting technologies that use low frequency mechanical energy to enhance data collection [85, 86]. Second, the current lightweight housing design suffered from substantial premature failures; this was primarily due to the combined influence of the thin layer of epoxy applied (especially in small individuals) and the rocky environment inhabited by the study species, necessitating further optimization when future studies involve harsh environments. For example, laminating the epoxy layer with a fiberglass mesh would help resist abrasion and prevent crack propagation. Third, reliance on physical data download precludes real-time monitoring capabilities in the current model. Integrating Internet of Things (IoT) technology for wireless transmission is a key future direction to facilitate more dynamic conservation efforts [87]. Despite these constraints, the demonstrated methodological approach presents a valuable and scalable framework for gathering behavioral data on elusive species in a budget- and user-friendly fashion, paving the way for deeper ecological insights for understudied species.

Conclusion

By employing an innovative methodological approach using purpose-built accelerometers in open-source environments, we demonstrate that monitoring the activity profiles and locomotory behaviors of small- to medium-sized animals is both possible and cost effective. Featuring this in a highly elusive freshwater turtle, this study further underscores the critical role of innovative biologging technologies, such as accelerometry, in advancing our understanding of the behavioral patterns of cryptic and elusive animals, like *P. megacephalum* and many other freshwater turtle species. Our findings regarding the activity cycle of *P. megacephalum* and the potential impacts of extreme weather events underscore the potential vulnerability of *P. megacephalum* to ongoing and future anthropogenic disturbances. The results also highlight the urgency of targeted conservation efforts if we are to safeguard the long-term viability of this distinct species. Through a deeper understanding of the mechanistic links underlying how intrinsic behavioral attributes are connected to extrinsic environmental threats, we can now foster effective conservation strategies that directly mitigate the risks of population decline and extinction and preserve biodiversity in the face of changing environmental conditions.

Abbreviations

CL	Carapace length
PL	Plastron length
DBA	Dynamic body acceleration
ODBA	Overall dynamic body acceleration
HMM	Hidden Markov model
EM	Expectation maximization
GAM	Generalized additive model
IoT	Internet of things

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-026-00460-6.

Supplementary Material 1.

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Author contributions

Conceptualization: YHS, WSC, Methodology: WSC, Software: BK, WSC, Formal analysis: WSC, Investigation: WSC, YHS, Resources: YHS, Data curation: WSC, Writing – Original Draft: WSC, Writing – Review & Editing: all authors, Visualization: WSC, Supervision: TCB, YHS, Project administration: TCB, YHS, Funding acquisition: YHS.

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Data availability

All relevant data and codes are publicly available in [https://github.com/wingsingChan/PLME_Accelerometry_Public](https:/github.com/wingsingChan/PLME_Accelerometry_Public) .

Declarations

Ethics approval and consent to participate

All sampling procedures were approved by the University animal ethics committee (Ref no: EC030/1920), the Department of Health (Ref no: (19–77) in DH/HT&A/8/2/8 Pt.1), and Agriculture, Fisheries, and Conservation Department (Ref no: (95) in AF GR CON 09/51 Pt.8, (3) in AF GR CON 09/51 Pt.8, and (86) in AF GR CON 09/51 Pt.7) of Hong Kong.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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