Fall 2023

Activity Patterns of the Critically Endangered Central American River Turtle (Dermatemys Mawii)

Cora Dyslin
Missouri State University, cd938s@missouristate.edu

Recommended Citation

Dyslin, Cora, "Activity Patterns of the Critically Endangered Central American River Turtle (Dermatemys Mawii)" (2023). *MSU Graduate Theses*. 3915.
https://bearworks.missouristate.edu/theses/3915

ACTIVITY PATTERNS OF THE CRITICALLY ENDANGERED CENTRAL AMERICAN RIVER TURTLE (*DERMATEMYS MAWII*)

A Master's Thesis
Presented to
The Graduate College of
Missouri State University

In Partial Fulfillment
Of the requirements for the Degree
Master of Science, Biology

By
Cora Dyslin
December 2023

ACTIVITY PATTERNS OF THE CRITICALLY ENDANGERED CENTRAL AMERICAN RIVER TURTLE (*DERMATEMYS MAWII*)

Biology

Missouri State University, December 2023

Master of Science

Cora Dyslin

ABSTRACT

The Central American River Turtle (*Dermatemys mawii*) is native to southern Mexico, eastern Guatemala, and Belize and is primarily restricted to watersheds that drain into the Gulf of Mexico and Caribbean Sea. Hunting, both for personal consumption and market meat, has been the primary driver of declines, and the species is now classified as critically endangered. Results from past studies that have used netting and visual surveys to detect *D. mawii* suggest that the species is chiefly nocturnal. However, it is unclear to what extent the perception of nocturnality has been biased by the timing of survey efforts (e.g., animals may appear to be nocturnal if efforts to detect them are restricted to nighttime surveys). A more detailed understanding of activity patterns is important, in part because it informs many other aspects of the species' biology (foraging patterns, environmental effects, etc.), but also because understanding when individuals are most likely to be moving can help to inform hunting regulations and research efforts. Therefore, to quantify the daily and seasonal activity patterns of *D. mawii* in a natural river system in Belize, I equipped 8 males, 8 females, and 8 juveniles with archival dataloggers to record acceleration (movement), temperature, and pressure (water depth), and sonic transmitters to aid in relocating and recapturing turtles. Over the course of five sampling trips, from June 2021 to July 2022, I recaptured and downloaded data from 18 of the 24 tagged individuals, resulting in intervals of consecutive data for each turtle ranging from 1–13 months. Surprisingly, and contrary to previous assertions that the *D. mawii* are chiefly nocturnal, my results indicate that this species exhibits a crepuscular activity pattern, with lowest rates of activity occurring at night. Overall, males were more active than juveniles, which were more active than females. Additionally, I observed a distinct seasonal pattern in activity for males and females, with higher levels of nocturnal activity in the rainy season and higher levels of diurnal activity during the dry season. Temperature negatively correlated with activity, and depth was positively correlated with activity, suggesting *D. mawii* are more active at greater depths and cooler temperatures. Additionally, females spend more time at greater depths than males or juveniles, and all three demographic groups go deeper during the dry season.

KEYWORDS: activity, accelerometer, conservation, *Dermatemys*, diel

ACTIVITY PATTERNS OF THE CRITICALLY ENDANGERED CENTRAL AMERICAN RIVER TURTLE

(*DERMATEMYS MAWII*)

By
Cora Dyslin

A Master's Thesis
Submitted to the Graduate College
Of Missouri State University
In Partial Fulfillment of the Requirements
For the Degree of Master of Science, Biology

December 2023

Approved:

Day B. Ligon, Ph.D., Thesis Committee chair

Sean P. Maher, Ph.D., Committee Member

Donald T. McKnight, Ph.D., Committee Member

Julie Masterson, Ph.D., Dean of the Graduate College

TABLE OF CONTENTS

Introduction Page 01

Methods Page 04
  Study site Page 04
  Data collection Page 05
  Activity measurement Page 06
  Data analyses Page 06
  Statistical analyses Page 07

Results Page 10
  Demographic group, season, and time of day Page 11
  Environmental effects on activity Page 12
  Depth, activity, and demographic group Page 13

Discussion Page 14
  Diel and seasonal activity patterns Page 14
  Rainfall and activity Page 17
  Temperature and water depth effects on activity Page 18
  Submersion Page 18
  Conservation implications Page 19

Literature Cited Page 20

Appendix Page 37

LIST OF TABLES

Table 1. Summary of retrieved data Page 25

LIST OF FIGURES

Figure 1. Map of Turtle Creek Page 26
Figure 2. Photo of a tagged *D. mawii* Page 27
Figure 3. Visual of data collected Page 28
Figure 4. GAM plot of activity across demographics Page 29
Figure 5. Activity between demographics, season, and time of day Page 30
Figure 6. Acceleration between demographics, season, and time of day Page 31
Figure 7. Activity and rainfall Page 32
Figure 8. Activity and water temperature Page 33
Figure 9. Activity and depth Page 34
Figure 10. Depth between demographics, season, and time of day Page 35
Figure 11. Maximum submersion time Page 36

INTRODUCTION

Studies of animal activity patterns are becoming increasingly prevalent in population management and conservation efforts (Bridges and Noss 2011, Hays et al. 2019, Yeap et al. 2022). Understanding the activity patterns of animals can elucidate individual and population level patterns and processes which, in turn, can inform management strategies and reveal conservation priorities (Murchie et al. 2011, Rayner et al. 2011). For example, a species being more active during the day or night has substantial impact on other aspects of their ecology, including predation type and risk (Kappeler and Erkert 2003). Behavioral patterns can also predispose species to threats from overharvesting. Researchers utilized activity data of the critically endangered freshwater river shark, *Glyphis glyphis*, to demonstrate that the movement patterns of these sharks make them particularly susceptible to overexploitation by fishing gear such as gill nets and baited hooks (Pillans et al. 2009). Localized movement patterns of this species suggest that small-scale management, in addition to education efforts of recreational and commercial fishers, would be the most effective management strategy (Pillans et al. 2009).

Traditionally, activity data have been collected through direct observations, which often render *in situ*, long-term studies impractical. The development of biotelemetry and acceleration data loggers has allowed researchers to change the way they study *in situ* animal ecology by providing detailed, continuous information on multiple aspects of species' biology, such as behavior, spatial ecology, energetics, and physiology, while virtually eliminating the potential of observer effects caused by human presence (Bograd et al. 2010, Brown et al. 2013, Whitney et al. 2021). Moreover, this technology has made it possible to collect detailed life-history information of cryptic species, such as aquatic animals, that do not allow for direct observation approaches (Wilson and McMahon 2006, Hussey et al. 2015).

Biologgers have been used in conservation research more frequently since the early 2000s (Cooke 2008). In combination with sensors, this technology can reveal information about habitat use and environmental factors such as temperature, depth, and dissolved oxygen of free-ranging animals in their natural habitat (Bograd et al. 2010, Wilson et al. 2014, Williams et al. 2019). Biologging also allows detailed study of wild animals, rather than moving individuals with reproductive potential to captivity—a particularly impactful characteristic for endangered populations (Cooke 2008). Finally, biologgers and accelerometers provide the opportunity to use an individual-based approach in ecological studies, with each device associated with a specific, recognized individual, rather than random, unrecognized individual encounters being used to infer a population-based characteristic or response (Ropert-Coudert et al. 2009).

A species' activity patterns can provide insight into its life history and behavior (Helm et al. 2017, Levy et al. 2016). Variation in diel and seasonal activity patterns can be a result of temporal partitioning (i.e., being active during time periods with minimal predation risk and optimal foraging potential), physiological constraints such as thermoregulation, or endogenous factors such as health condition or reproductive state (Kronfeld-Schor and Dayan 2003, Glorioso and Cobb 2012). Some species are specifically adapted for certain diel periods (Cooper 1999, Hall and Ross 2006, Land and Nilsson 2012), whereas others are capable of being active during multiple periods of the day (Kronfeld-Schor and Daya 2003, Hut et al. 2012, Levy et al. 2016, Lassiter et al. 2022). Many species exhibit seasonal changes in diel activity patterns as a response to changes in temperature, food availability, or changing water levels (Fraser et al.

1993, Kronfeld-Schor and Dayan 2003, Boal and Giovanni 2007, Sperry et al. 2013, Davimes et al. 2017, Lassiter et al. 2022). Although freshwater turtles are known to demonstrate seasonal plasticity in activity patterns, influences of diel activity patterns are not well understood (Smith and Iverson 2002, Ennen et al. 2008, Tucker et al. 2015, Lassiter et al. 2022). Furthermore, knowledge of diel and seasonal activity patterns and potential temporal plasticity can help inform conservation management decisions (Culling et al. 2003, Levy et al. 2019 Gallo et al. 2022). Therefore, activity patterns, and understanding how they change throughout the year, are an important component of not only a species' fundamental biology, but management practices for that species as well.

The Central American river turtle, *Dermatemys mawii* is a critically endangered freshwater species native to southern Mexico, eastern Guatemala, and Belize, and it is the only extant species of the Dermatemydidae family (Iverson and Mittermeier 1980). This species is fully aquatic and never basks, with females only briefly leaving water to lay their eggs (Briggs-Gonzalez 2019). They are most closely related to both mud and musk turtles of the Kinosternidae family (Zug 1966, Carr et al. 1981, Briggs-Gonzalez et al. 2019, Thomson et al. 2021). This fully herbivorous turtle species inhabits deep, cool waters such as slow-moving rivers and lagoons, and moves into seasonal floodplains and forests when water levels rise (Moll 1989, Vogt et al. 2011, Briggs-Gonzalez et al. 2019). Typical straight-line carapace lengths for male and female *D. mawii* range from 330 to 450 millimeters and 340 to 480 millimeters, respectively, and both sexes range 5.8–15 kg (Briggs-Gonzalez et al. 2019, Ligon et al. 2019). Mating season is thought to occur from April through mid-September, followed by nesting season, which takes place at the peak of the rainy season (Polisar 1996, Briggs-Gonzalez et al. 2019).

Hunting, both for personal consumption and market meat, has been the primary driver of *D. mawii* declines. *Dermatemys mawii* are thought to be most active at night, and is when most hunting takes place (Alvarez del Toro 1979, Vogt et al. 2006, Anleu et al. 2010, Vogt et al. 2011). However, much remains to be understood about both diel and seasonal activity patterns of this species, and examining these patterns will help to inform aspects of the natural history, physiology, and behavior.

I measured the activity of 24 wild *D. mawii* throughout a calendar year using archival data loggers to better understand the activity cycles of this cryptic species. I quantified differences in activity between demographic groups, time of day, and season, analyzed the effects of water temperature and rainfall on activity, and tested whether males and females vary in activity patterns and habitat use. Finally, I quantified submersion time among *D. mawii* individuals.

METHODS

Study site — This study was approved by the Missouri State University IACUC (protocol 2021-10; Appendix) and Belize Fisheries Department (permit 0019-21) on May 21st, 2021. The study took place from June 2021 to July 2022 in a series of riverine pools located in northwestern Belize, hereafter referred to as 'Turtle Creek' (per Ligon et al. 2019) to mask its location from potential poachers. Recent surveys have shown that Turtle Creek supports a viable and demographically healthy population of *D. mawii,* as it is dominated by sexually mature individuals (Ligon et al. 2019). The creek runs through a large section of forest and consists of multiple deep pools (maximum = 4.5 m) punctuated by shallow riffles (<0.2 m) that likely limit movement of *D. mawii* between pools (Ligon et al. 2019). For location reference, each pool within the creek was assigned letter designations, and my study was conducted in pools E–I (Figure 1). This segment of Turtle Creek was approximately 15 m across and consisted of tannic water with low turbidity, patchy soft and rocky substrate that included both cobble and large boulders, abundant fallen trees and submerged logs, and trees overhanging into the water (Ligon et al. 2019). A sample of 24 turtles—8 mature females, 8 mature males, and 8 juveniles (whose sex could not be determined form external morphological characters) was captured in June 2021 using trammel nets and free diving hand capture methods. Juveniles were defined as individuals that lacked identifiable secondary sex characteristics and were less than 350 mm SCL.

Data collection — During an initial sampling trip in June 2021, each of the 24 *D. mawii* composing the study population were equipped with an archival data logger (model MCFT3, Lotek Wireless, Inc., Newmarket, Ontario, Canada) and an acoustic transmitter (model CT-82-2-E, Sonotronics, Tucson, AZ, USA) to track and recapture individuals to download data from the archival loggers. Using twine, cyanoacrylate glue, and waterproof epoxy, I affixed the acoustic transmitter and archival data logger as a single unit to the posterior portion of the carapace (Figure 2). I drilled two small holes (~2 mm) through the 10th and 12th right marginal scutes to secure the transmitter and data logger with twine to prevent potential equipment loss that could occur when turtles shed their scutes (McKnight et al. 2023). To minimize the effects of transmitters on the turtles, I ensured that the combined mass of the logger, transmitter, and epoxy did not exceed 5% of body weight. The combined mass was an average of 50.33 g, and never exceeded 52 g. The smallest turtle in the sample population was a juvenile that weighed 1000 g during the initial capture in June 2021.

Using scuba equipment and a handheld diving receiver (model UDR, Sonotronics, Tucson, AZ, USA), tagged individuals were located and recaptured periodically over six sampling trips to download stored data from the archival loggers. Nonfunctioning data loggers were identified during download sessions and were subsequently removed from the turtle's carapace. In addition to the tagged individual *D. mawii*, I attached a single archival data logger to a large rock to serve as a control. At the end of the study, I removed the acoustic transmitter and data logger from all recaptured individuals. Due to a combination of data logger failure and inability to recapture some individuals, few turtles provided a full 12 months of data (Figure 3).

Activity measurement — The archival data loggers recorded activity using a tri-axial accelerometer programmed to summarize acceleration at 36-second intervals, resulting in 100 readings per hour. The activity sensor ran at an internal sample rate of 12.5 Hz. The logger computed an Act–V_{sum} value (g) for each sampling interval (36 seconds) by taking the maximum of all the internal samples and logs for each of the axes (X, Y, and Z), squaring those maxima, adding them together, and taking the square root of the sum. This value represented the rate of acceleration for that 36 second interval. In addition to acceleration, each logger also recorded pressure and temperature readings at the same frequency, and data loggers were calibrated to translate pressure readings to depth. To assess activity levels, I used data from the control data logger to identify a lower limit for Act–$V_{sum} > 0.02$ g for a point to qualify as "active".

Data analyses —Analyses were designed to test for differences among demographic groups (male, female, juvenile), differences between seasons (rainy and dry), and differences among times of day (diurnal, nocturnal, and crepuscular), as well as associations between activity and both rainfall and depth. Rainy and dry season dates for June 2021–July 2022 were determined from daily rainfall data collected by a weather station at Gallon Jug Ranch, approximately 14 km south of Turtle Creek. For these analyses, 12 June 2021 (initial sample population capture date) through 31 October 2021 represented the 2021 rainy season followed by dry season from 01 November 2021 through 26 May 2022. The 2022 rainy season start date was 27 May 2022 and continued through the end of sampling in July 2023. I removed individuals from analyses of seasonal patterns that returned less than thirty days of data for a given season.

I grouped the data into three diel periods (diurnal, nocturnal, and crepuscular) to test for diel activity patterns. The periods of the day were determined from daily sunrise and sunset times. Crepuscular hours were defined as the four hours bracketing sunrise and sunset (i.e., sunset and sunrise ± 2 hrs), diurnal periods as the roughly eight hours between sunrise and sunset crepuscular periods, and nocturnal periods as the roughly eight hours between sunset and sunrise crepuscular periods (the exact number of hours for diurnal and nocturnal periods varied slightly as sunrise and sunset times changed seasonally). Dates were recorded using a "night of" date format, with each date starting at the beginning of the morning crepuscular period rather than midnight (e.g., a nocturnal period that actually started on 1 June and ran to the morning of 2 June was recorded entirely as 1 June, rather than splitting it into two dates). This is a more appropriate representation of a 24-hour cycle for *D. mawii*.

Statistical analyses —Because of the large number of data points collected, it was necessary to combine the data into summary statistics per individual per time of day (diurnal, nocturnal, crepuscular) per date (night of) and run analyses on those summary statistics. Summary statistics included: total number of data points, activity prevalence (i.e., number of data points [36-second intervals] when a turtle was active [ActV-Sum > 0.02g]), activity intensity (i.e., mean ActV-Sum when a turtle was active [ActV-Sum > 0.02g]), mean depth, and mean temperature. All mentions of “activity” in these analyses refer to changes in movement direction and acceleration.

All statistical analyses were performed using R Statistical Software (v4.2.2; R Core Team 2021), and significance was assessed using the Anova() function in the car package (v3.1-2; Weisberg 2019) with a Type II sums of squares. When significant interactions were present, results are visualized and discussed separately for the different levels of the interacting factors. Several types of models were used based on data structure and comparisons of model types using AIC. Anytime a linear model was used, assumptions were additionally checked using QQ plots and residual plots using the performance package (v0.10.5; Lüdecke et al. 2023). To account for differences in the total number of data points in each category, I included the natural log of the total number of data points as an offset in all activity models.

First, I compared activity patterns among seasons, demographics, and among times of day, looking at both the relative amount of time during which turtles were active and the average intensity of activity (amount of acceleration). To analyze the relative number of active acceleration readings ($\text{Act–V}_{\text{sum}} > 0.02\text{g}$) among periods of the day, demographics, and season, I ran a random intercept mixed effects hurdle model using a truncated negative binomial distribution via the glmmTMB package (v0.1.3; Magnusson et al. 2017). Number of active points (per individual, per date, per diel period) was included as the response variable, turtle identification and date (night of) were included as random effects, demographic, period of the day, season, and all possible interactions between those three were included as fixed effects, and the natural log of the total number of data points was included as an offset. To further visualize the diel patterns among demographics and between seasons, I plotted the results of a smoothed general additive model with the data summarized per hour, rather than per time of day (diurnal, nocturnal. crepuscular) (Figure 4).

To analyze the intensity of activity solely when the turtles are active, I ran a linear random intercept mixed effects model with turtle identification number and date as random effects, and demographic, period of the day, season, and any possible interactions between those three as fixed effects. Mean activity (ActV-Sum) was included as the response variable following a power transformation to meet model assumptions. Data were transformed by raising them by -1.4225 based on the transformTukey function in the rcompanion package (v2.4.34; Mangiafico 2023).

To test for a relationship between rainfall events and activity (rather than simply rainy season vs dry season), I subset the data to the rainy season and ran a random intercept mixed effects hurdle model using a truncated negative binomial distribution with turtle identification number and date as random effects and demographic, total rainfall on that date, and their interaction as fixed effects. The number of active points was the response variable, and the natural log of the total number of data points was an offset. I also used the same model to analyze the effect of rainfall over the previous 24 hours on activity with the substitution of rainfall over the previous 24 hours for night-of rainfall as a fixed effect.

I used random intercept mixed effects hurdle model using a truncated negative binomial distribution to analyze the effect of water temperature on the count of active points for each demographic group. Turtle identification number and date were assigned as random effects, and demographic, temperature, and their interaction were assigned as fixed effects. The dataset was subset to the most active hour of each day (0600) and the model was run on this subset. Autocorrelation was not accounted for. Temperature ranged 24–32°C, but only 7% of the data points were below 25°C or above 28°C; therefore, out of concern that those extreme points might bias the results, I ran the same model twice, once using the full temperature range, and once using only data points from 25–28°C.

To analyze the effect of depth on the count of active points, I ran a random intercept mixed effects hurdle model using a truncated negative binomial distribution with turtle identification number and date as the random effects, and demographic, depth, and their interaction as fixed effects. Again, the dataset was subset to the most active hour of each day (0600) and the model was run on this subset dataset. Autocorrelation was not accounted for.

I used a random intercept mixed effects model using a negative binomial distribution to analyze potential differences in commonly inhabited depths among demographic groups. Pressure was the response variable, and turtle identification and date were assigned as random effects. Demographic, time of day, season, and any possible interactions among those three variables were assigned as fixed effects. Finally, maximum submersion time was determined by creating a cutoff of 1 meter as potentially breathing at the surface and analyzing how long individuals continuously remained deeper than 1 meter from the surface.

RESULTS

I collected activity, water depth, and temperature data from 18 individuals out of the 24 tagged turtles, with individual datasets ranging from 1 to 12 months (Table 1). Recapture rates decreased each sampling trip due to both technical issues with the transmitters, as well as accessibility issues within the river system. Six tagged *D. mawii* (2 females, 1 male, and 3 juveniles) were never detected post release in June 2021. Overall, I obtained more data during the initial 2021 rainy season months (02 June 2021–31 October 2021) than the dry season or subsequent rainy season (01 November 2021–26 May 2022 and 27 May 2022–31 October 2022 respectively).

Demographic group, season, and time of day effects on activity — Based on the relative amount of time (number of points) during which turtles were active, there were effects of time of day ($X^2 = 2347.08$, df = 2, $P < 0.0001$), demographic ($X^2 = 43.83$, df = 2, $P < 0.0001$), and season ($X^2 = 245.41$, df = 2, $P < 0.0001$) on the activity of *D. mawii* (Figures 4 and 5). However, many interactions were present, including a three-way interaction between demographic, time of day, and season ($X^2 = 115.06$, df = 4, $P < 0.0001$), making it difficult to make broad generalizations (Figure 4). Time of day produced the clearest patterns, with the highest level of activity consistently occurring during crepuscular periods for each demographic group in each season. There was also a generally strong effect of demographic group, with males being active more often than juveniles, which in turn were active more often than females (Figures 4 and 5). This pattern of differences among demographics was generally true across seasons and times of day, with the exception of nocturnal periods, during which the trend was present but not statistically significant during the rainy season (based on 95% CIs of fitted effects (Figure 5). Additionally, males were active less often than juveniles in the dry season.

The effects of season were complex. During diurnal hours, all demographic groups were active more often during the dry season than during the rainy season, but during nocturnal and crepuscular hours, males and females were active more often during the rainy season, while juveniles were active more often in the dry season (some of those differences were small and likely not significant on their own; see Figure 5). Stated another way, there was a distinct seasonal pattern in activity for males and females, with higher levels of nocturnal and crepuscular activity in the rainy season and higher levels of diurnal activity during the dry season (Figure 5), while juveniles were consistently more active during the dry season.

Based on the average acceleration rate during times when turtles were active (i.e., intensity of activity), there were effects of demographic (X^2 = 67.11, df = 2, $P < 0.0001$), time of day (X^2 = 914.92, df = 2, $P < 0.0001$), and season (X^2 = 5.22, df = 1, $P = 0.02$) (Figure 6). However, many interactions were once again present, including a three-way interaction between demographic, time of day, and season (X^2 = 64.85, df = 4, $P < 0.0001$), rendering it difficult to make broad generalizations. Differences among demographics produced the clearest result, with females consistently exhibiting the highest rates of acceleration, followed by males, then juveniles (Figure 6). This pattern of differences among demographic groups was generally true across periods of the day and seasons. All three demographics exhibited the highest acceleration rates during nocturnal hours in both the rainy and the dry season. Seasonal patterns were also present (with interactions). During nocturnal hours, all three demographics had higher mean acceleration rates during the dry season than during the rainy season, whereas in the diurnal period, the pattern flipped with higher average acceleration during the rainy season (Figure 6). Acceleration rates during crepuscular periods of the day remained relatively consistent across seasons (Figure 6).

Environmental effects on activity — Rainfall on a given date had no significant effect on activity and no significant interactions were present ($X^2 = 2.58$, df = 1, $P = 0.11$) (Figure 7). Additionally, when looking at the effect of rainfall over the previous 24 hours on activity, there was no effect and no significant interactions were present ($X^2 = 0.06$, df = 1, $P = 0.81$) (Figure 7). Water temperature negatively correlated with relative amount of time a turtle was active (count of active points) as a main effect when the full range of water temperature was considered (24–32°C) ($X^2 = 16.78$, df = 1, $P < 0.0001$) as well as when outlier temperatures were excluded and only the common range of temperatures (25 – 28°C) were considered ($X^2 = 18.60$, df = 2, $P < 0.0001$)(Figure 8). There were no significant interactions between demographic group and temperature for the full range model ($X^2 = 0.98$, df = 2, $P = 0.6113$). However, there was an interaction between demographic and temperature for the main range model ($X^2 = 136.66$, df = 3, $P < 0.0001$).

Depth, activity, and demographic group — The relative amount of time a turtle was active (count of active points) was significantly higher for all three demographic groups as depth increased ($X^2 = 141.51$, df = 1, $P < 0.0001$) (Figure 9). No significant interactions were present between demographic and water depth ($X^2 = 0.66$, df = 2, $P = 0.7204$). The depth at which turtles spent most of their time varied with time of day ($X^2 = 229.05$, df = 2, $P < 0.0001$) and season ($X^2 = 20.89$, df = 1, $P < 0.0001$) (Figure 10). However, multiple interactions were present, including a three-way interaction of demographic, time of day, and season ($X^2 = 21.38$, df = 4, $P = 0.0003$), making it difficult to draw broad conclusions. Despite the lack of main effects, in general, females inhabited deeper water, on average, than the other demographic groups. All three demographics usually occupied greater mean depths during the dry season than in the rainy season (Figure 10), and all three groups inhabited shallower mean depths during nocturnal hours than crepuscular or diurnal hours (Figure 10).

In the interest of finding maximum submersion time, I set a threshold for potential submersion when loggers were deeper than 1 m. This is inherently conservative because it is possible that *D. mawii* could be submerged for prolonged intervals at shallower depths, but it is difficult to eliminate instances of turtles lifting their heads to the surface even as the posterior-oriented loggers remain deep. As a result, summary statistics such as means and medians are not useful because *D. mawii* individuals may be less than 1 m deep but not actually at the surface breathing. However, looking at extreme values is useful for understanding maximum submersion potential. Of 230,911 recorded submersion events, 99% of submersion events lasted less than one hour and 0.08% of intervals lasted 1–2 hours. 131 submersion events lasted longer than 2 hours, with a maximum duration of 76 hours (Figure 11).

DISCUSSION

Diel and seasonal activity patterns — Previous studies have reported that *D. mawii* is a nocturnal species based on visual surveys and trapping (Alvarez del Toro et al. 1979, Anleu et al. 2010, Briggs-Gonzalez et al. 2019). However, my results suggest that nocturnality inaccurately describes the typical diel activity patterns of this species, with activity patterns revealed by this study more closely fitting a bimodal pattern that is roughly consistent with a crepuscular pattern of activity. Previous trapping and survey efforts were done predominantly at night (Moll 1986, Rainwater et al. 2012, Ligon et al. 2019, McKnight et al. 2021), potentially influencing the assumption that *D. mawii* is chiefly nocturnal.

Activity of freshwater turtles is noted to be temperature-dependent, and many species tend to exhibit unimodal activity patterns at colder water temperatures and bimodal activity at warmer water temperatures (Graham 1979, Graham and Hutchison 1979, Glorioso and Cobb 2012, Singh 2018). However, with air and water temperatures remaining above 20°C in my study system, temperatures may have been warm enough to support a bimodal activity cycle year-round. Similarly, some Australian chelids, including *Myuchelys bellii*, exhibit a crepuscular activity pattern during spring, summer, and autumn when temperatures are warmer, and a diurnal activity pattern during the winter when temperatures drop (Gordos and Franklin 2002, Fielder 2012).

It is important to acknowledge that this crepuscular description of activity may fail to capture nuances that deviate from the bimodal pattern. Despite the results from this study, this fully herbivorous species has been visually observed foraging at night on several occasions across several years (Moll 1986, Moll 1989, Vogt et al. 2011, Briggs-Gonzalez 2019). However, foraging may require minimal movement or acceleration, as *D. mawii* feed on overhanging or fallen leaves and emergent vegetation (Vogt et al. 2011, Briggs-Gonzalez 2019). It has also been noted that when waters rise and inundate shorelines, both adult and juvenile *D. mawii* will relocate to grass beds shortly after sundown to graze throughout the night (Moll 1989). Moreover, *D. mawii* are noted to become active at twilight after resting during the day (Alvarez del Toro et al. 1979). These observations are supported by my results demonstrating increased movement during crepuscular periods and minimal movement during nocturnal hours. It is difficult to infer behavior from the activity data, and it is possible that ecologically important behaviors that require little movement fit a different temporal pattern than ascribed by acceleration data. Diel patterns of activity among males, females, and juveniles were consistent in shape, but activity plots varied in amplitude. Males were generally more active than females at nearly all times, and this pattern was particularly pronounced during diurnal hours.

Despite being active the least often, females exhibited the highest rates of acceleration during periods of activity. In other words, when females are active, they demonstrated a tendency to move very quickly compared to males and juveniles. It is possible that females accelerated quickly to escape male harassment, and males may seldom give chase to a female in flight mode. All three demographic groups exhibited higher rates of acceleration during nocturnal hours despite being overall less active during the night. A study of activity patterns of *Sternotherus odoratus* demonstrated that individuals tend to exhibit some degree of movement throughout the diel cycle, suggesting they are not strictly diurnal, nocturnal or crepuscular (Rowe et al. 2009). The high rates of acceleration at night might result from moving greater distances using an alternating accelerate-glide movement pattern. Another possibility is that increased acceleration rates at night may be due to evasive maneuvers to avoid predators, as one of their primary predators, the Morelet's Crocodile (*Crocodylus moreletii*), primarily hunts at night (Moll 1986, Platt et al. 2006, Briggs-Gonzalez et al. 2019). Finally, increased flightiness at night may result from individuals being more easily startled and fleeing areas quickly when visibility is limited due to low light levels.

The rainy season in Belize is approximately May through October, and males and females both exhibited higher levels of diurnal activity during the dry season and higher levels of nocturnal activity during the rainy season. Nesting likely occurs from mid-September through December (Polisar 1996, Vogt et al. 2011, Briggs-Gonzalez 2019), coinciding with the increase in diurnal activity seen in my results. A possible explanation for the increase in female diurnal activity during the dry season is the shift from mating season to nesting season when females exit the water to lay their eggs along the banks of the river. As suggested by the reproductive strategies hypothesis, males tend to exhibit greater activity levels than females during the mating season (Morreale et al. 1984, Litzgus and Mousseau 2004). However, this hypothesis also posits that females will tend to have equal or greater activity than males during the nesting season. Male *D. mawii* exhibited consistently higher levels of relative activity compared to females throughout the entire year, and this increased activity may reflect different levels of activity associated with reproduction such as mate searching and courtship. Male *D. mawii* have been observed circling around stationary females during mating season, potentially contributing to the higher levels of activity seen in this study (D. Ligon personal communication). Another potential explanation could be the decreased abundance of food available for foraging during the dry season (Vogt et al. 2011). Foraging is thought to occur predominantly at night, possibly correlating to the increased levels of nocturnal activity during the rainy season when food is more abundant (Briggs-Gonzalez 2019). However, my results suggest that the species follows a more complex pattern that varies seasonally and is best classified as crepuscular with seasonally varying rates of diurnal and nocturnal activity.

Rainfall and activity —With the onset of rainy season, *Dermatemys mawii* are known to disperse and leave lagoons isolated by low water levels during the dry season (Briggs-Gonazalez 2019). Moreover, the species is reported to increase activity levels and foraging efforts at any time of day during periods of water level increase (Moll 1986, 1989, Polisar 1996, Vogt et al. 2011). Surprisingly, my results failed to detect an increase in activity during or immediately following rain events. I expected to see increased activity levels after rainfall based on anecdotal data from time in the field (D. Ligon personal communication), but perhaps *D. mawii a*ctivity levels are influenced solely by water level changes rather than actual rainfall, and only a subset of rain events are large enough to produce substantial changes in depth. If so, activity may only increase during particularly large rainfall events, rather than a general correlation with rainfall. Finally, it is also possible that previous anecdotal reports were simply wrong and resulted from observation bias rather than actual patterns of activity.

Temperature and water depth effects on activity — Dermatemys mawii has been reported to prefer deeper, cooler water and will often rest on the bottom and even partially submerge in soft substrate (Alvarez del Toro et al. 1979, Vogt et al. 2011). Furthermore, captive *D. mawii* have been noted to remain deep as they move throughout their enclosures rather than swimming near the surface (Campbell 1972). Recent trammel net surveys support this assessment, as the majority of captured *D. mawii* were caught in the bottom half of 3-m deep nets (A. Grate unpublished data). Temperature negatively correlated with activity for all three demographic groups in this study. Additionally, activity was higher at greater depths for all three demographics, suggesting that *D. mawii* are more active at the cooler bottom of the water system than at the surface. Overall, my results support the consensus in the literature that *D. mawii* spend significant time in deep water which may be due to cooler temperatures or predator avoidance. However, rather than mostly resting at the bottom or resting in loose substrate (Briggs-Gonazlez et al. 2019), my results suggest that *D. mawii* individuals are more active at the bottom than previously recognized.

Submersion — The longest continuous submersion time that I recorded was over 76 hours, more than an order of magnitude longer than >99% of submersion events. The pharynx of *D. mawii* contain vascularized papillae, structures that have been hypothesized to facilitate aquatic gas exchange and support prolonged submersion (Winokur 1988, Vogt et al. 2011). However, this prolonged submersion pattern is not typical for freshwater turtles. Studies have shown that other freshwater turtle engage in voluntary submersion bouts lasting less than 20 minutes, with only 2% of submersions persisting >50 minutes (Stone et al. 1992). *Dermatemys mawii* have been reported to congregate in large underwater holes; however, because it is possible for such holes to have air pockets, it is unclear to what extent this behavior depends on great capacity for prolonged submersion (Alvarez del Toro et al. 1979).

Conservation implications — Dermatemys mawii is frequently poached using gill nets and trammel nets, methods of capture that depend on turtles actively swimming and getting entangled. However, poachers are not the only ones capturing *D. mawii* with gill or trammel nets, as researchers also use these capture methods. My results suggest that daytime and crepuscular periods may be more productive intervals than the more typical nighttime sessions that have often typified survey efforts. This inference should be validated in a study that follows a 24-hour trapping schedule, as it is conceivable that specific nocturnal behaviors that do not trigger high rates of movement nonetheless increase trapability. Moreover, my results suggest that males may be more susceptible to capture in nets than females, a pattern that may contribute to biased estimates of population sizes and sex ratios. Finally, it is clear that survey time needs to be taken into account when comparing survey results across years or locations, as differences in capture rates could reflect seasonal and diel biases rather than true differences in turtle abundance.

LITERATURE CITED

Anleu, R.G., Vogt, R., McNab, R.B., Moreira, J., Santizo, G.P., Mérida, M., Ruano, G., González, E. Muñoz, E., Córdova, M., and Bosarreyes, B. 2010. Where do they go? Determining the spatial and habitat requirements of the CA River Turtle (*Dermatemys mawii*: Dermatemidae) in El Perú Lagoon, Selva Maya of Guatemala. Technical Report.

Alvarez del Toro, M., Mittermeier, R.A., and Iverson, J.B. 1979. River turtle in danger. Oryx 15:170–173.

Boal, C. W., and Giovanni, M. D. 2007. Raptor predation on Ord's kangaroo rats: evidence for diurnal activity by a nocturnal rodent. Southwestern Naturalist 52:291–295.

Bograd, S.J., Block, B.A., Costa, D.P., and Godley, B.J. 2010. Biologging technologies: new tools for conservation. Endangered Species Research 10:1–7.

Bridges, A.S. and Noss, A.J. 2011. Behavior and Activity Patterns. Camera Traps in Animal Ecology: 57–69.

Briggs-Gonzalez, V., Gonzalez, S.C., Smith, D., Rainwater, T.R., and Mazzotti, F.J. 2019. Species profile for the Hicatee (*Dermatemys mawii*). Caribbean Naturalist 2:156–176.

Brown, D.D., Kays, R., Wikelski, M., Wilson,R., and Klimley, A.P. 2013. Observing the unwatchable through acceleration logging of animal behavior. Animal Biotelemetry: 1–20.

Campbell, J. 1972. Observations on Central American River Turtles (*Dermatemys mawii*) at Fort Worth Zoo. Zoo yearbook 12:202–204.

Carr, J.L., Bickham, J.W., and Dean, R.H. 1981. The karyotype and chromosomal banding patterns of the Central American River Turtle, *Dermatemys mawii*. Herpetologica 37:92–95.

Cooke, S.J. 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endangered Species Research 4:165–185.

Cooper, W. E. 1999. Prey chemical discrimination in ambush foragers: absence in representatives of two additional Iguanian lizard families and probable olfactory mediation in a gekkonine gecko. Chemoecology 9:155–159.

Culling, M.A., Valero, I.L., and Cóté, I.M. 2003. Substratum preferences and diel activity patterns of Spined Loach *Cobitis taenia* in England: implications for conservation management. Folia Biologica 51:129–133.

Davimes, J. G., Alagaili, A.N., Bertelsen, M.F., Mohammed, O.B., Hemingway, J., Bennett, N.C., Manger, P.R., and Gravett, N. 2017. Temporal niche switching in Arabian oryx (*Oryx leucoryx*): seasonal plasticity of 24h activity patterns in a large desert mammal. Physiology and Behavior 177:148–154.

Ennen, J.R., and Floyd, S.A. 2008. Diel Movement Behavior of The Stripe-Necked Musk Turtle (*Sternotherus Minor Peltifer*) in Middle Tennessee. The American Midland Naturalist 160:278-288.

Fielder, D.P. 2012. Seasonal and diel dive performance and behavioral ecology of the bimodally respiring freshwater turtle *Myuchelys bellii* of eastern Australia. Journal of Comparative Physiology 198:129–143.

Fraser, N.H.C., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Series B: Biological Sciences 252:135–139.

Gallo, T., Fidino, M., Gerber, B., Ahlers, A.A., Angstmann, J.L., Amaya, M., Drake, D., Gay, D., Lehrer, E.W., Murray, M.H., and Ryan, T.J., 2022. Mammals adjust diel activity across gradients of urbanization. Elife 11:e74756.

Glorioso, B.M., and Cobb, V.A. 2012. Diel and temporal activity indicated by feeding in the Eastern Musk Turtle, *Sternotherus odoratus*, at Reelfoot Lake, Tennessee. Herpetological Conservation and Biology 7:323–329.

Gordos, M.A., Franklin, C.E. 2002. Diving behaviour of two Australian bimodally respiring turtles, *Rheodytes leukops* and *Emydura macquarii*, in a natural setting. Journal of Zoology 258:335–342.

Graham, T. E. 1979. Locomotor activity in the Blanding's turtle, *Emydoidea blandingii* (Reptilia, Testudines, Emydidae): The phasing effect of temperature. Journal of Herpetology 13:365–366.

Graham, T.E., and Hutchison, V.H. 1979. Turtle diel activity: Response to different regimes of temperature and photoperiod. Comparative Biochemistry and Physiology Part A: Physiology 63:299–305.

Hall, M. I., and Ross, C. F. 2006. Eye shape and activity pattern in birds. Journal of Zoology 271:437–444.

Hays, G.C., Bailey, H., Bograd, S.J., Bowen, W.D., Campagna, C., Carmichael, R.H., Casale, P., Chiardia, A., Costa, D.P., Cuevas, E., Nico de Bruyn, P.J., Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., and Sequeira A.M.M. 2019. Translating marine animal tracking data into conservation policy and management. Trends in Ecology and Evolution 34:459–473.

Helm, B., Visser, M. E., Schwartz, W., and Kronfeld-Schor, N. 2017. Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. Philosophical Transactions of the Royal Society B: Biological Sciences 372: 20160246.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocki, J.F., Flemming, J.E.M., and Whoriskey, F.G. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1–10.

Hut, R.A., Kronfeld-Schor, N., der Van Vinne, V., and De la Iglesia, H. 2012. In search of a temporal niche: environmental factors. Progress in Brain Research 199:281–304.

Iverson, J.B., and Mittermeier R.A. 1980. Dermatemydidae, *Dermatemys* Gray. Catalogue of American publications of the Society for the Study of Amphibians and Reptiles 237:1–4.

Kappeler, P.M. and Erkert, H.G. 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild Redfronted Lemurs (*Eulemur fulvus rufus*). Behavioral Ecology and Sociobiology 54:359–369.

Kronfeld-Schor, N., and Daya, T. 2003. Partitioning of time as an ecological resource. Annual review of ecology, evolution, and systematics 34:153–181.

Land, M.F., and Nilsson, D.E. 2012. Animal eyes. 2nd ed. Oxford University Press, Oxford.

Lassiter, E.V. 2022. Seasonal patterns in activity and occupancy dynamics of the imperiled spotted turtle (*Clemmys guttata*). Doctoral dissertation, University of Arkansas.

Levy O., Dayan, T., Porter, W.P., and Kronfeld-Schor N. 2016. Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. American Naturalist 188:205–218.

Levy, O., Dayan, T., Porter, W.P., and Kronfeld-Schor, N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? Ecological monographs 89:e01334.

Ligon, D.B., McKnight, D.T., Thompson, D.M., Hollender, E.C., and Marlin, J.A. 2019. The Development of Protocols and Training for Population Estimates of the Central American River Turtle (*Dermatemys mawii*) in the Spanish Creek/Belize River Watershed Key Biodiversity Area. Final Report to PACT, The World Bank, and The Government of Belize.

Litzgus, J.D., and Mousseau, T.A., 2004. Home range and seasonal activity of Southern Spotted Turtles (*Clemmys guttata*): implications for management. Copeia 4:804–817.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. (2021). Performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of R package version 6:3139.

Magnusson, A., Skaug, H.J., Nielsen, A., Bert, C.W., Kristensen, K., Maechler, M., van Bentham, K.J., Bolker, B.M., and Brooks, M.E. 2017. glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R package version 0.1.3.

Mangiafico, S.S. 2023. Rcompanion: Functions to Support Extension Education Program Evaluation. Rutgers Cooperative Extension. R package version 2.4.34.

McKnight, D.T., Serano, J.C., Thompson, D.M., and Ligon, D.B. 2023. They really do move in herds: evidence of group living in an aquatic turtle. Animal Behavior article in press.

McKnight, D.T., Thompson, D.M., Ligon, D.B., Serano, J.C., Pop, P., Marlin, J.A., and Barrett, H. 2021. Population ecology and conservation of *Dermatemys mawii* in Belize. Final Report, Belize Fisheries Department.

Moll, D. 1986. The distribution, status, and level of exploitation of the freshwater turtle *Dermatemys mawii* in Belize, Central America. Biological Conservation 35:87–96.

Moll, D. 1989. Food and feeding behavior of the turtle, *Dermatemys mawii*, in Belize. Journal of Herpetology 23:445–447.

Morreale, S.J., Gibbons, J.W., and Congdon, J.D. 1984. Significance of activity and movement in the Yellow-Bellied Slider Turtle (*Pseudemys scripta*). Canadian Journal of Zoology 62:1038–1042.

Murchie, K.J., Cooke, S.J., Danylchuk, A.J., and Suski, C.D. 2011. Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. Journal of Experimental Marine Biology and Ecology 396:147–155.

Pillans, R.D., Stevens, J.D., Kyne, P.M., and Salini, J. 2009. Observations on the distribution, biology, short-term movements and habitat requirements of River Sharks *Glyphis* spp. In northern Australia. Endangered Species Research 10:321–332.

Platt, S.G., Rainwater, T.R., Finger, A.G., Thorbjarnarson, J.B., Anderson, T.A., and McMurry, S.T. 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behavior of Morelet's Crocodile (*Crocodylus moreletii*) in northern Belize. Herpetological Journal 16:281–290.

Polisar, J. 1996. Reproductive biology of a flood-season nesting freshwater turtle of the northern neotropics: *Dermatemys mawii* in Belize. Chelonian Conservation and Biology 2:13–25.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainwater, T.R., Pop, T., Cal, O., Garel, A., Platt S.G., and Hudson, R. 2012. A recent countrywide status survey of the critically endangered Central American River Turtle (*Dermatemys mawii*) in Belize. Chelonian Conservation and Biology 11:97–107.

Rayner, M.J., Taylor, G.A., Thompson, D.R., Torres, L.G., Satar, P.M., and Shaffer, S.A. 2011. Migration and diving activity in three non-breeding Flesh-footed Shearwaters *Puffinus carneipes*. Journal of Avian Biology 42:266-270.

Ropert-Coudert, Y., Beaulieu, M., Hanuise, N., and Kato, A. 2009. Diving into the world of biologging. Endangered Species Research 10:21-27.

Rowe, J.W., Lehr, G.C., McCarthy, P.M., and Converse, P.M. 2009. Activity, movements, and activity area size in Stinkpot Turtles (*Stenrotherus odoratus*) in a southwestern Michigan lake. The American Midland naturalist 162:266–275.

Singh, K. 2018. Ecology of the Macquarie turtle (*Emydura macquarii macquarii*) downstream of a large hypolimnetic-releasing impoundment in Australia's southern Murray-Darling Basin. Doctoral dissertation, Charles Sturt University.

Smith, G.R., and Iverson, J.B. 2002. Sex ratio of Common Musk Turtles (*Sternotherus odoratus*) in a north- central Indiana lake: a long-term study. American Midland Naturalist 148:185–189.

Sperry, J., Ward, M.P., and Weatherhead, P.J. 2013. Effects of temperature, moon phase, and prey on nocturnal activity of Ratsnakes. Journal of Herpetology, 47:105–111.

Stone, P.A., Dobie, J.L., & Henry, R.P. 1992. The Effect of Aquatic O_2 Levels on Diving and Ventilatory Behavior in Soft-Shelled (*Trionyx spiniferus*), Stinkpot (*Sternotherus odoratus*), and Mud Turtles (*Kinosternon subrubrum*). Physiological zoology 65:331–345.

Thomson, R.C., Spinks, P.Q., and Shaffer H.B. 2021. A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. Proceedings of the National Academy of Sciences 118:e2012215118.

Tucker, C.R., Strickland, J.T., Edmond, B.S., Delaney, D.K., and Ligon, D.B. 2015. Activity Patterns of Ornate Box Turtles (*Terrapene ornata*) in Northwestern Illinois. Copeia 103:502–511.

Vogt, R.C., G.P. Gonzalez-Porter, and P.P. Van Dijk. 2006. *Dermatemys mawii* (errata version published in 2016). *The IUCN Red List of Threatened Species* 2006: an online reference. Available at https://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T6493A12783921.en.

Vogt, R.C., Polisar, J.R. Moll, D., and Gonzalez-Porter, G. 2011. *Dermatemys mawii* Gray 1847 – Central American River Turtle, Tortuga Blanca, Hickatee. Chelonian Research Monographs 5:1–12.

Weisberg, F.J. 2019. An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA.

Whitney, N.M, White, C.F., Smith, B.J., Cherkiss, M.S., Massoti, F.J., and Hart, K.M. 2021. Accelerometry to study fine-scale activity of invasive Burmese Pythons (*Python bivaittatus*) in the wild. Animal Biotelemetry 9:1–13.

Wickham, H., Francois, R., Henry, L., Müller, K., and Vaughan, D. 2023. Dplyr: A Grammar of Data Manipulation. R package version 1.1.3.

Williams, H.J., Taylor, L.A., Benhamou, S., Bijleveld, A.I., Clay, T.A., Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Laich, A., Griffiths, R.C., Kay, W.P., Morales, J.M., Potts, J.R., Rogerson, K.F., Rutz, C., Spelt, A., Trevail, A.M., Wilson, R.P., and Börger, L. 2019. Optimizing the use of biologgers for movement ecology research. Journal of Animal Ecology 89:186–206.

Wilson, R.P., Grundy, E., Massy, R., Soltis, J., Tysse, B., Holton, M., Cai, Y., Parrott, A., Downey, L.A., Qasem, L., and Butt, T. 2014. Wild state secrets: ultra-sensitive measurement of micro-movement can reveal internal processes in animals. Frontiers in Ecology and the Environment 12:582–587.

Wilson, R.P. and McMahon, C.R. 2006. Measuring devices on wild animals: what constitutes acceptable practice? Frontiers in Ecology and the Environment 4:147–154.

Winokur, R.M. 1988. The buccopharyngeal mucosa of the turtles (Testudines). Journal of Morphology 196:33–52.

Yeap, L., Warren, K.S., Bouten, W., Vaughan-Higgins, R., Jackson, B., Riley, K., Rycken, S., and Shephard, J.M. 2022. Application of tri-axial accelerometer data to the interpretation of movement and behaviour of threatened Black Cockatoos. Wildlife Research 49:100–110.

Zug, G.R. 1966. The penial morphology and the relationships of cyprtodiran turtles. Occasional papers of the Museum of Zoology 347:1–24.

Table 1. Summary of data retrieved from the 24 tagged *D. mawii* individuals. The “Months of Data” column lists the total number of months of data that has been successfully downloaded from that logger. Straight carapace length (SCL) is measured in mm, and mass is measured in grams.

Turtle ID	Sex	Months of Data	SCL	Mass
DM43434	F	1	394	8500
DM43486	M	1	373	6350
DM43448	J	1	321	4000
DM77706	J	1	249.5	1920
DM63124	F	2	422.5	8850
DM43499	M	2	406.5	7900
DM87507	M	2	398	7600
DM71208	F	3	419	9000
DM71168	M	3	362	5800
DM71212	F	5	415	8400
DM67352	J	7	214.4	1300
DM58387	M	9	411.5	8250
DM71163	M	9	378	6225
DM91010	F	11	378.5	7100
DM66179	F	12	425	9800
DM43439	M	12	379	6450
DM43445	J	12	328	4500
DM71240	J	13	193.2	1025
DM67308	F	x	359	6100
DM71220	F	x	368.5	6400
DM71183	M	x	360	6350
DM71169	J	x	226.1	1500
DM71210	J	x	305	3500
DM77748	J	x	184.5	1000

Figure 1. Designated pools within the Turtle Creek system. Pool D is not easily accessible to *D. mawii* and was not included in the sampling area where study animals were collected.

Fig. 2. Juvenile *D. mawii* with newly affixed data logger and acoustic transmitter coated in waterproof epoxy. Photo credit: C. Dyslin.

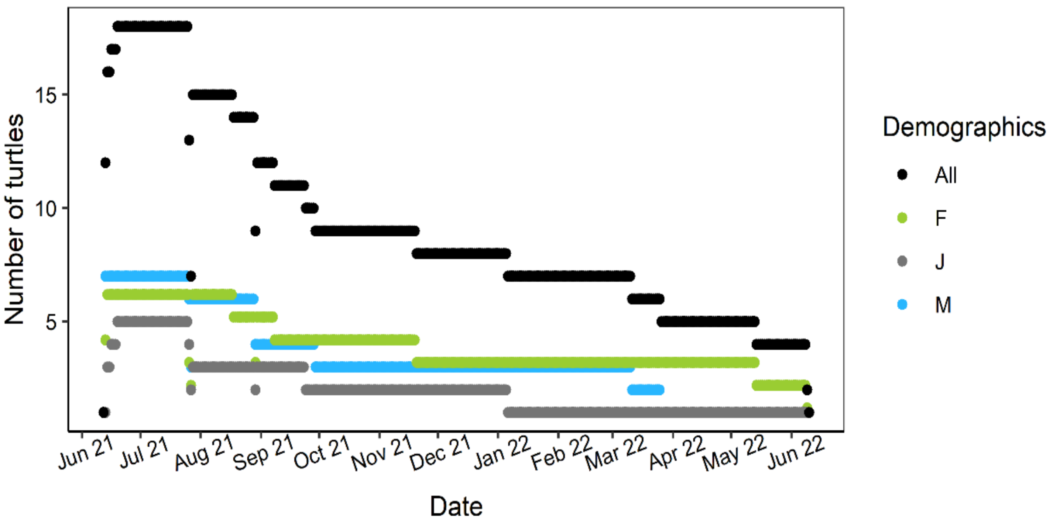

Fig. 3. Visual representation of data collected from the 18 recaptured *D. mawii*. Data were obtained from individuals for intervals ranging 1–12 months.

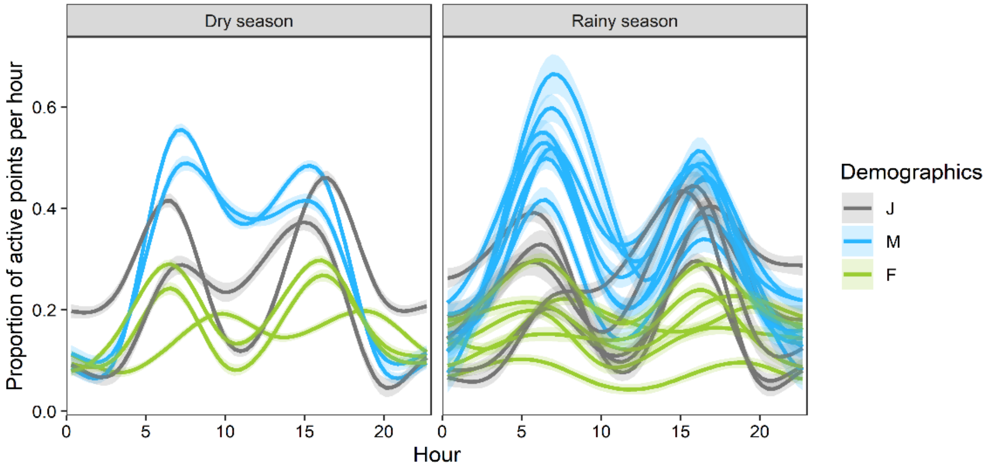

Fig. 4. Smoothed GAM line plot showing proportion of points during which *D. mawii* were active (Act-$V_{sum} > 0.02$ g). Shading represents 95% confidence intervals. Plots were made in ggplot2 (v.3.4.3; Wickham et al. 2023).

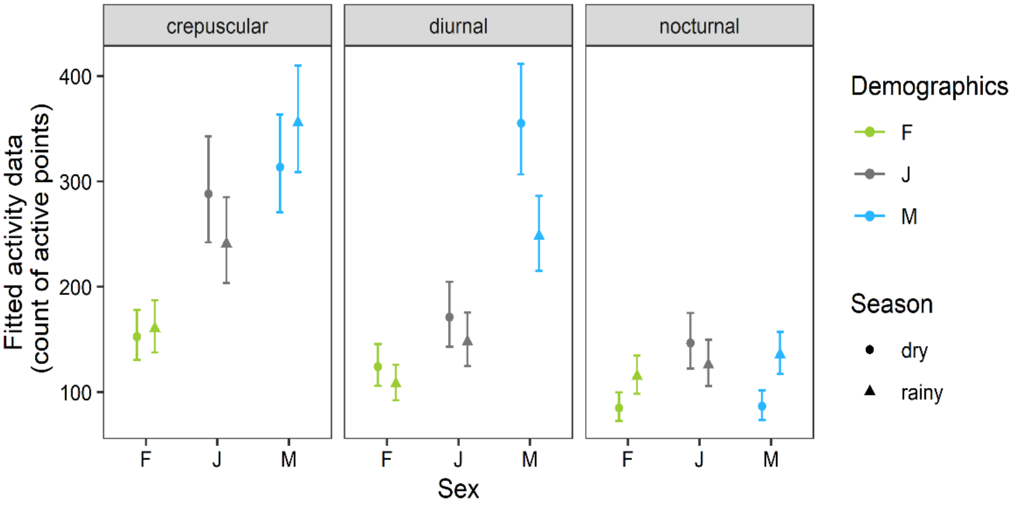

Fig. 5. Fitted effects from the random intercept mixed effects hurdle model comparing the amount of time during which *D. mawii* were active (number of active points [Act-V_{sum} > 0.02 g], with total number of points included as an offset) among demographic groups, times of day, and seasons. Error bars represent 95% confidence intervals.

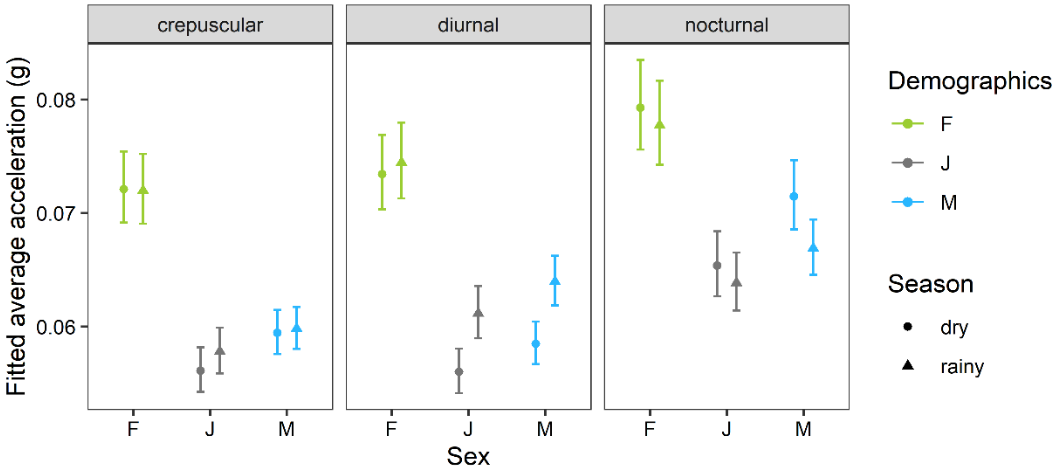

Fig. 6. Fitted effects from the random intercept mixed effects model comparing the rate of *D. mawii* acceleration (with the total number of points included as an offset) among time of day, demographic groups, and seasons. Error bars represent 95% confidence intervals.

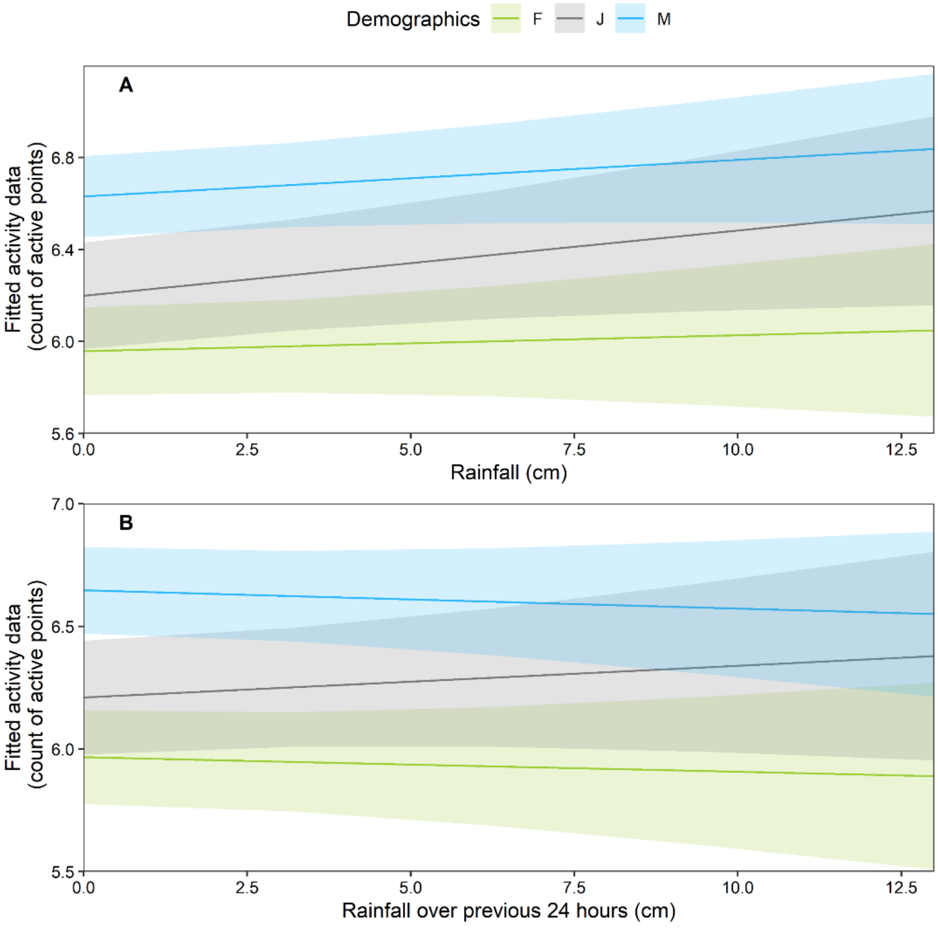

Fig. 7. Fitted effects from the random intercept mixed effects hurdle model examining the relationship between the count of active points for *D. mawii* (acceleration > 0.2 g) and active rainfall (A) and rainfall over the previous 24 hours (B). Shading around the lines represent 95% confidence intervals.

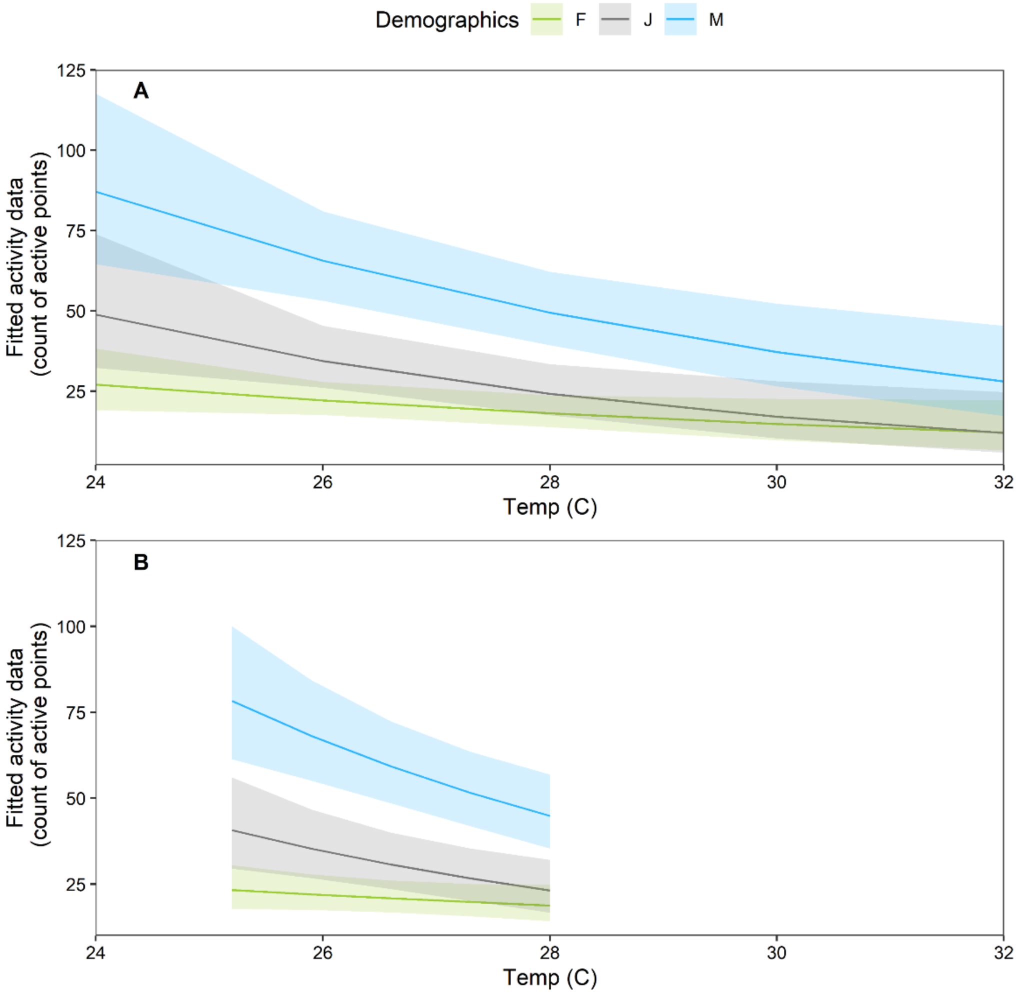

Fig. 8. Fitted effects from the random intercept mixed effects hurdle model examining the relationship between the count of active points for *D. mawii* (Act-V_{sum} reading over 0.02 g) and water temperature (full range [A], main range with outlier temperatures removed [B]) with the total number of points included as an offset. Shading around the lines represent 95% confidence intervals.

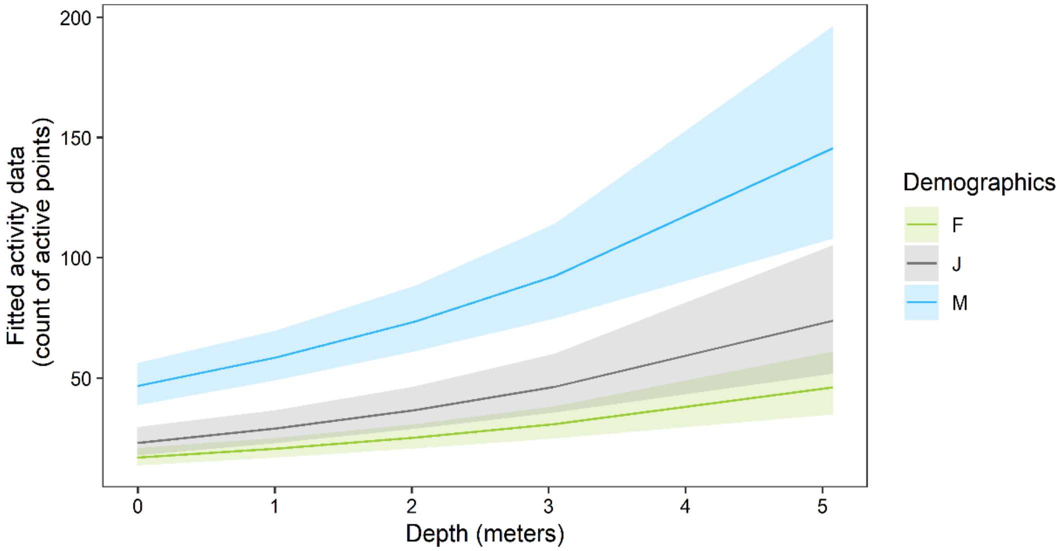

Fig. 9. Fitted effects from the random intercept mixed effects hurdle model examining the relationship between activity (Act-V_{sum} reading over 0.02 g) and depth, with the total count of points included as an offset. Shading represents 95% confidence intervals.

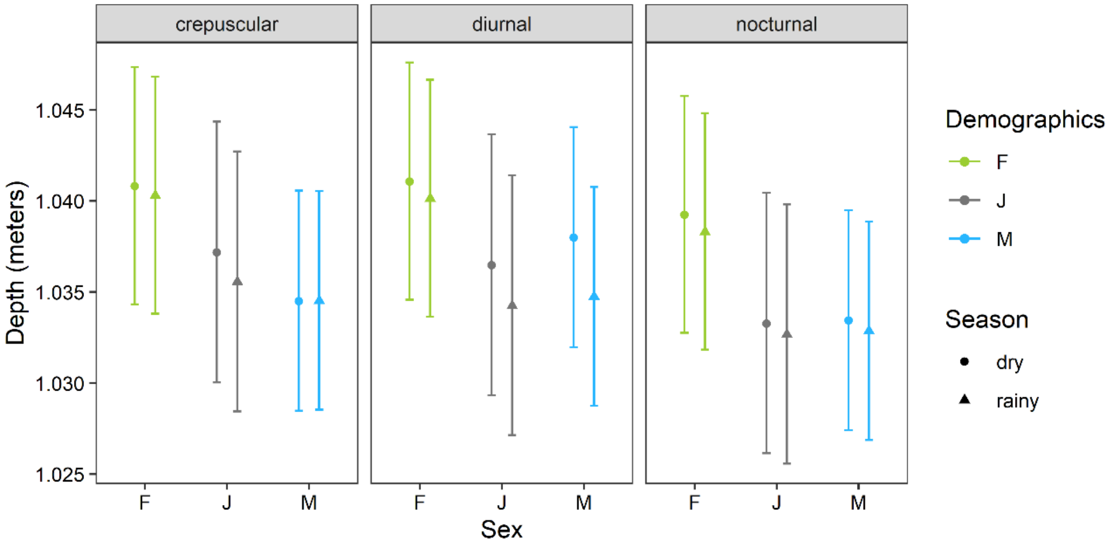

Fig. 10. Fitted effects from the random intercept mixed effects model examining the relationship between *D. mawii* depth, demographic group, time of day, and season. Bars represent 95% confidence intervals.

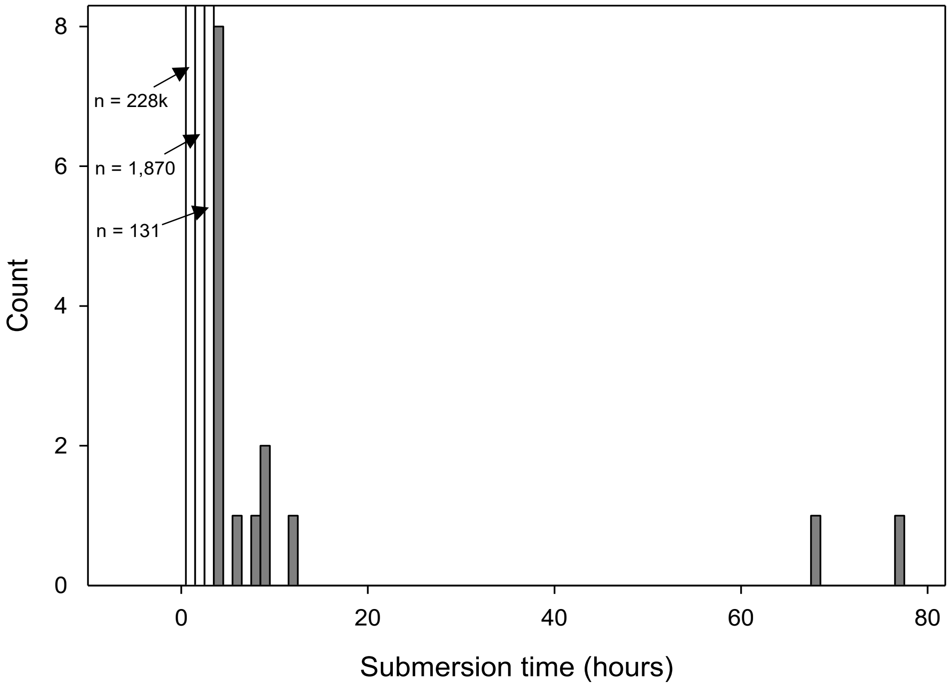

Fig. 11. Count of *D. mawii* submersion events between 0 and 77 hours calculated using a minimum threshold of 1 m below the surface. The maximum submersion time recorded exceeded 76 hours.

APPENDIX

All research methods were approved by the Missouri State University Institutional Animal Care and Use Committee in May of 2021 (see protocol 2021-10 below).

Missouri State
UNIVERSITY

October 2, 2023

RE: IACUC protocol 2021-10

Cora Dyslin,

IACUC protocol #2021-10 entitled "Surveys of *Hicatee* (and other aquatic turtles) in Belize" was approved by the committee on May 21, 2021 and expires May 20, 2024.

The protocol reflects that you are approved to work with Dr. Day Ligon on this project.

Thank you and if you need anything in the future regarding this protocol, please contact me either via email (johnnapedersen@missouristate.edu) or at 417-836-3737.

Sincerely,

Johnna Pedersen

Johnna Pedersen
IACUC Administrator/Member
Interim Director of Research Administration