Presence And Temporal Activities Of Serrated Hinged Terrapin (Pelusios sinuatus) And Marsh Terrapin (Pelomedusa galeata) In KwaZulu-Natal, South Africa, Assessed Using Telemetry

Authors: Price, Cormac, Burnett, Matthew J, O'Brien, Gordon, and Downs, Colleen T

Source: Tropical Conservation Science, 15(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/19400829221074241

Research Article

Tropical Conservation Science
Volume 15: 1–15

Article reuse guidelines:
sagepub.com/journals-permissions
DOI: 10.1177/19400829221074241
journals.sagepub.com/home/trc
SAGE

Presence And Temporal Activities Of Serrated Hinged Terrapin (*Pelusios sinuatus*) And Marsh Terrapin (*Pelomedusa galeata*) In KwaZulu-Natal, South Africa, Assessed Using Telemetry

Cormac Price[1], Matthew J Burnett[1], Gordon O'Brien[1,2] and Colleen T Downs[1]

Abstract

Background and Aims: For the first time in Africa, two freshwater turtle species (hereafter terrapin**)** presence and temporal activity in their habitats were investigated using radio telemetry.

Methods: Telemeter tags were attached to *Pelusios sinuatus* (*n* = 10) at Ndumo Reserve and *Pelomedusa galeata* (*n* = 10) at Tala Reserve. *Pelusios sinuatus* tagged individuals were monitored between August–December 2016 at Ndumo, while *P. galeata* individuals were monitored between November 2017–July 2018 at Tala. Sensors on the tag determined the tag temperature and temporal activity. We examined both species' frequency distributions of inactivity to time of day. Activity trends for both species in comparison with ambient temperature and tag temperature were analyzed.

Results: Tags showed individuals presence or absence as detected by fixed remote networks at the study sites. Tagged *P. sinuatus* in Ndumo disappeared after a flood without returning after the flood receded. Both species were diurnal, with *P. galeata* showing a greater ability to maintain tag temperature above ambient temperature in the first 10 h of a day than *P. sinuatus*. Climatic data, including ambient temperature, rainfall, and wind, were retrieved from weather stations. The most significant climatic variable that affected activity was ambient temperature. Rainfall also showed a significant effect, but wind showed no significant effect.

Implications for Conservation: This method can become a valuable tool for long-term remote monitoring of other semi-aquatic reptiles in wetlands that are increasingly under anthropogenic and climatic pressure. Thus, its implications for conservation are significant.

Keywords
Africa, reptiles, *Pelomedusidae*, wetlands, turtle crisis, wildlife monitoring

Introduction

Globally, wetlands and other aquatic environments are changing rapidly because of anthropogenic pressures, including land-use change and climate change. In turn, this has a significant effect on the species that inhabit them, in particular their temporal movements and activities (Hussey et al., 2015). Climate change has caused climatic patterns to become increasingly difficult to predict but typically have more

[1]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Scottsville, South Africa
[2]School of Biology and Environmental Sciences, University of Mpumalanga, South Africa

Received: 18 October 2021

Corresponding Author:
Colleen T Downs, Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Scottsville, 3209, South Africa.
Email: downs@ukzn.ac.za

frequent, extended droughts and extreme temperatures (Abbas et al., 2019). Rainfall patterns have become more erratic and are predicted to continue being more irregular, and the frequency of flash flooding is set to increase (IPCC, 2021; Kusangaya et al., 2018). Anthropogenic pressures alter wetland habitats in various ways, from a general reduction in size to changing the flow regimes, affecting the water quality and the habitat variability (Rodell et al., 2018). Conservation measures are urgently needed for several wetland species living in regions of the world where field research is curtailed by logistic or economic constraints (Luiselli, 2008; Hocutt et al., 1994).

Turtles are among the most threatened vertebrate taxa globally (Lovich et al., 2018; Gibbons and Lovich, 2019). Furthermore, freshwater turtles (hereafter terrapins) are typically undervalued as important ecosystem components in the habitats they are found (Doody et al., 2009; Price et al., 2021). Due to the constraints and the challenges of working in remote wetland habitats, new techniques and methods must be tested to achieve the most accurate form(s) of data collection (Luiselli, 2008). Climate change is expected to alter water availability and natural temperature ranges, affecting how semi-aquatic ectotherm species regulate their temperature, find suitable micro-habitats, and thus potentially threaten their survival (Bowen et al., 2005; Kusangaya et al., 2018, Chessman, 2019). However, little is known about how African terrapins respond to fluctuations in environmental variables within their environments. This challenge is further amplified by a lack of accurate and/or remote survey techniques in the field.

Terrapins play fundamental and ecologically essential roles within the ecological communities they are found. For example, terrapins can be predators (Rödel, 1999), prey for higher trophic species (Dalhuijsen et al., 2014), seed dispersers (Kimmons and Moll, 2010), as standing crops of biomass (Iverson, 1982), and indicators of ecosystem health (Basile et al., 2011). Although not traditionally considered an indicator species. Terrapins are long-lived (Howell et al., 2019) and typically maintain high levels of site fidelity (Pérez-Pérez et al., 2017), making them suitable indicator species.

An animal's continued presence, temporal activity patterns, and habitat use are in part determined by proximal factors, including the landscapes they occupy, seasonal or environmental cues and individual attributes such as sex and body size (Roe and Georges, 2008). Understanding species persistence and behavior in relation to their environment are essential to identify and mitigate conservation threats to the species (Famelli et al., 2016). This can help understand what they require within habitats to maintain stable populations (Famelli et al., 2016). The collection of biological information is fundamental to improving the understanding of the functioning of habitats and ecosystems so that these can be recognized, mitigated or averted to improve the conservation strategies (Ríos-Saldaña et al., 2018). This is particularly important for wetland species, such as terrapins, facing increased drought and flooding events (Price et al., 2021). Telemetry methods are frequently used to determine the temporal activity, movement and spatial ecology of both terrestrial and aquatic species; however, limitations because of body size, subject species and transmitter weight often constrain the use of these techniques (Thomas et al., 2011; Burnett et al., 2021). These limitations are being overcome by advances in technology, such as allowing the attachment of relatively small telemeter tags on terrapin and fish species to record their activity and movement (Gibbons and Lovich, 2019; Burnett et al., 2021). This has increased the understanding of different terrapin species' activity, spatial behavior and conservation, particularly in Australia (Roe and Georges, 2008; Doody et al., 2009; Pérez-Pérez et al., 2017; Gibbons and Lovich, 2019).

Behavioral and ecological studies on terrapins using telemetry methods have never been conducted in Africa. Telemetry techniques can be used to remotely monitor amphibious species movement between terrestrial and aquatic ecosystems and these species' behavioral ecology (Burnett et al., 2020; Calverley & Downs, 2015). Areas of South Africa, including KwaZulu-Natal, experienced the worst drought in about 50 years from 2014 to 2016 (Abbas et al., 2019), and this overlapped with the present study. These drought conditions inevitably impact the presence, temporal activity patterns, energy budgets, and general fitness of species, particularly amphibious ectothermic species, such as terrapin species. This affects such species' conservation if their natural habitats are adversely affected by drought and extreme flooding events. Therefore, telemeter tags are increasingly used to monitor free-ranging individuals remotely to show that they are still present and active in an area, even when they are visually unable to be detected or threatened by predation (Sonamzi et al., 2020).

The serrated hinged terrapin (*Pelusios sinuatus*, Smith, 1838) and the marsh terrapin (*Pelomedusa galeata,* Schoepff, 1792) occur in southern Africa (Bates et al., 2014a). *Pelomedusa galeata* appear to take advantage of anthropogenically altered landscapes, particularly where impoundments/dams are built (Vamberger et al., 2018; Vamberger et al., 2019a). The temporal activity in relation to environmental variables for both terrapin species is poorly understood. Our main aims were to understand better these species' continued presence and temporal activity in relation to their wetland environment and habitats using remote telemetry methods, especially in a changing climate. Our objectives were to attach radio telemetry tags to individuals of both species and set up a remote network of stations to collect the tag data in real-time reliably. We wanted to examine the terrapins' temporal activity regimes in relation to climatic variables. As terrapins are ectotherms, we hypothesized that their temporal movements (activity) are affected by climatic variables, especially temperature. We also predicted that the more coastal, tropical terrapin species *P. sinuatus* would have higher temperature preferences for increased activity. It is an East African species with its southern range limit in north-eastern coastal KwaZulu-Natal, South Africa (Vamberger et al., 2019b). In contrast, the more widespread generalist *P. galeata* also occurs in temperate, cooler, and drier habitats (Vamberger et al., 2019a).

Methods

Study Areas

Two study areas were selected, representing subtropical (Ndumo Game Reserve (hereafter Ndumo)) and cooler, more temperate, southeastern uplands (Tala Private Game Reserve (hereafter Tala)) in KwaZulu-Natal, South Africa. Ndumo (26°51′59.95″S 32°15′0.00″E; Figure 1) is an Ezemvelo KZN Wildlife protected area bordering Mozambique and is ~10,000 ha in size. It was proclaimed a RAMSAR site in 1997 because of the international importance and unique habitats and species associated with the wetlands found within the reserve (Whittington et al., 2013). It is in the sub-tropical region of South Africa with natural or near-natural wetlands characteristic of the Maputaland–Pondoland–Albany region (Grundling et al., 2013). Nyamithi Pan (a natural water body that can dry out during drought) was the focal point of the present telemetry research in Ndumo, extending ~4.2 km long and up to ~700 m wide (Pooley, 1982). Nyamithi's water sources, aside from rainfall, are primarily through backfilling from the Phongola or Usuthu Rivers' floodwaters via the outlet in an eastern periphery of the pan (Calverley and Downs, 2015). This pan was selected as a suitable site to implement a telemetry study as it is the largest permanent pan present, typically maintaining suitable terrapin habitat throughout the year (Calverley and Downs, 2014; Calverley and Downs, 2015).

Tala is situated south of Pietermaritzburg (29°49′32.61″S 30°32′29.69″E; Figure 2) and lies within the southeastern lowlands eco-region of KwaZulu-Natal Province (Fairbanks and Benn, 2000). The climate is temperate at 650–700 m

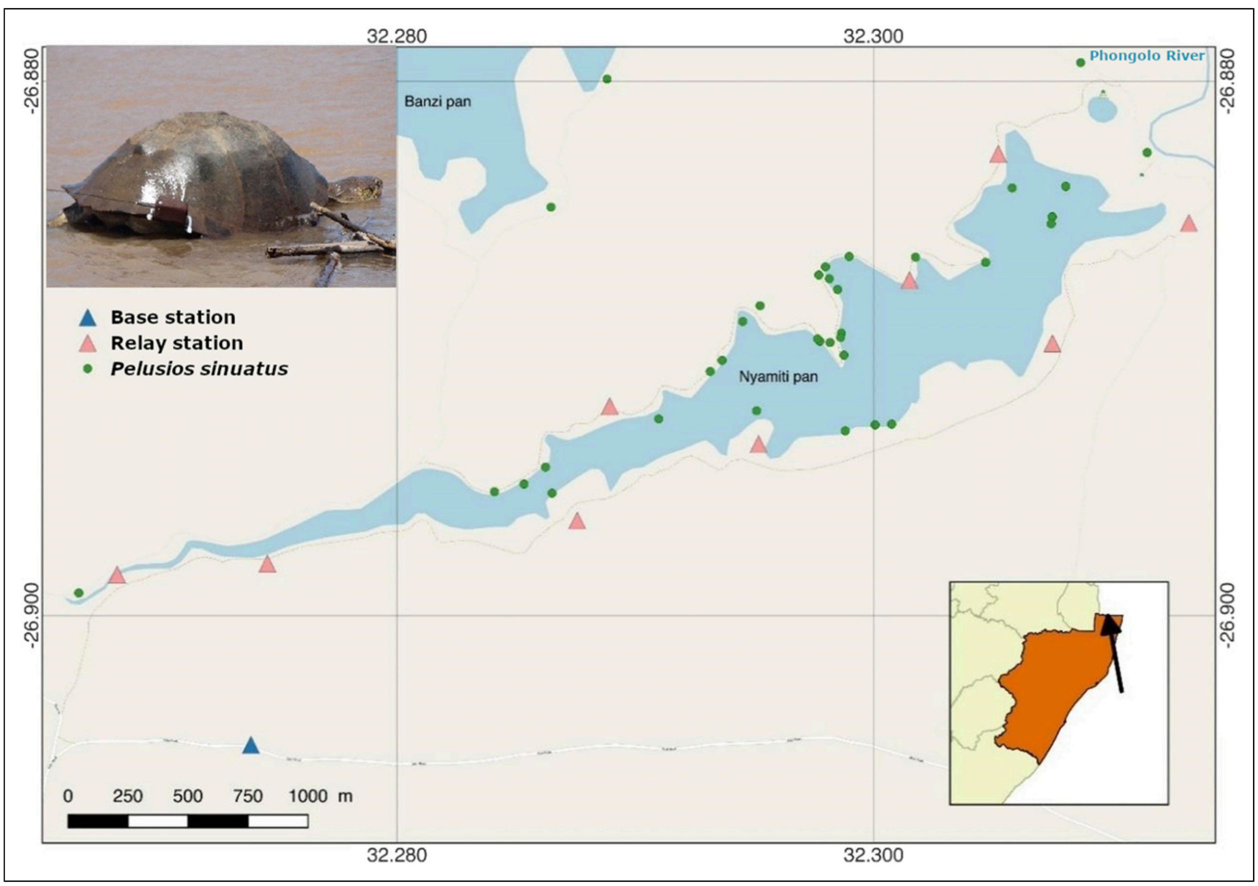

Figure 1. Map showing Nyamithi Pan, the focus site for *P. sinuatus* in Ndumo Game Reserve, KwaZulu-Natal Province, South Africa, indicating where terrapins were trapped, as well as where the receivers were installed. Insert shows KwaZulu-Natal Province, and the arrow indicates the location of Ndumo Game Reserve.

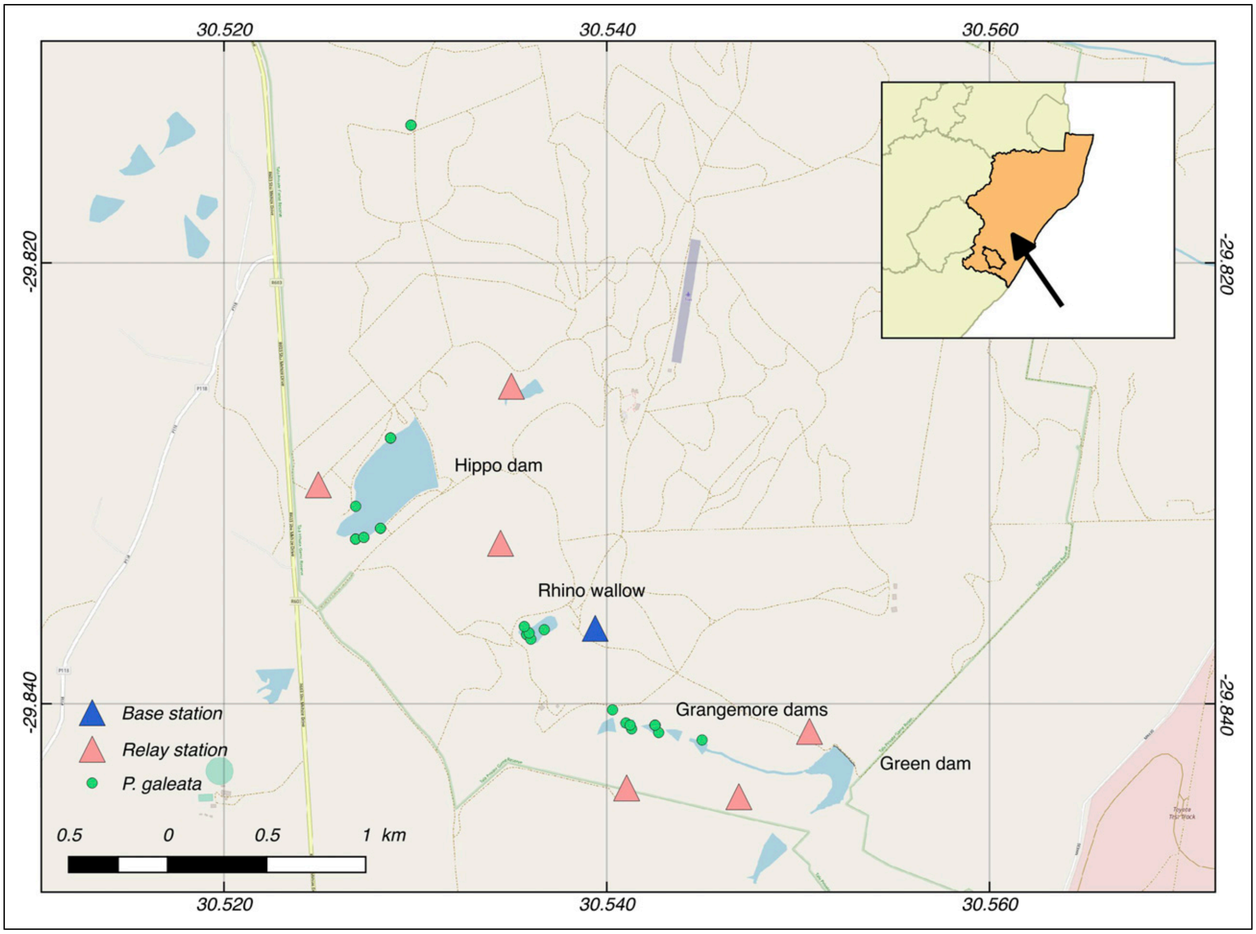

Figure 2. Map showing the focus wetlands at Tala Private Game Reserve, KwaZulu-Natal Province, South Africa, indicating where terrapins were trapped, as well as where the receivers were installed. Insert shows KwaZulu-Natal Province, and the arrow indicates the location of Tala Private Reserve.

above sea level. The reserve is a protected area of ~3,000 ha habitat surrounded by transformed natural areas used for agriculture and human settlements. Tala has a series of impoundments/dams, with the largest being ~655 m long and ~300 m wide, known as Hippo Dam (Figure 2). The dams are artificial earthen structures, and water levels depend on the catchment's annual rainfall (pers. comm. G. Allan, Manager, Tala Game Reserve, 2017). There are streams less than 2.5 km away from Tala's impoundments that feed into the Umhlatuzana River and its catchment area. The surrounding farmland has other impoundments relatively close by (pers. obs.; Humphries et al., 2016).

Tag Attachment and trapping

Given the novelty of this terrapin telemetry study in Africa, a laboratory trial was required to test the tag attachment technique on a terrapin. We attached a dummy telemeter tag with the exact dimensions of those used in the field to a *P. galeata* individual housed at the University of KwaZulu-Natal Animal House, Pietermaritzburg, KwaZulu-Natal, South Africa. For this experiment, we attached the dummy tag with plastic cable ties to the carapace's posterior above a hindleg, as planned with tag attachment on free-ranging terrapins. This was a similar but slightly modified tag attachment technique as used for the pig-nosed terrapin (*Carettochelys insculpta*) (Doody et al., 2009). Cable ties were chosen so that the telemeter tag could drop off the animal when they degraded enough. Thus, when the battery life expired, and the study was completed, the animal would not need to be recaptured, nor tags become permanent fixtures on the individuals. We placed this replica on the *P. galeata* individual in March 2016 and monitored it is behavior compared with five untagged individuals for 6 months before tagging in the field began in August 2016.

We used two types of traps to capture terrapins. Firstly, we used self-made wire-mesh traps (made by ourselves) (60 cm deep x 1 m long x 1 m wide), each with a one-way swinging trap door mechanism. The mesh used for these was 10 × 30 mm, ensuring no escapes. Secondly, we used commercial

Table 1. Details for the individual terrapins tagged in the present study, including tagging date, species and morphometric information. The number of days the tags transmitted information are also shown.

Date of tag attachment	Last recorded date	Species	Sex	Body mass (g)	Carapace length (mm)	Carapace width (mm)	No. of fixes	No. of days data were retrieved
21-Aug-16	14-Sep-16	*P. sinuatus*	Female	3,650	280	203	412	24
01-Nov-16	11-Dec-16	*P. sinuatus*	Female	8,040	380	272	765	40
16-Nov-16	24-Nov-16	*P. sinuatus*	Male	1,790	242	180	216	8
16-Nov-16	18-Nov-16	*P. sinuatus*	Female	5,200	322	248	48	2
16-Nov-16	12-Dec-16	*P. sinuatus*	Female	2,680	260	195	638	26
16-Nov-16	18-Nov-16	*P. sinuatus*	Female	5,970	330	248	45	2
12-Dec-16	13-Dec-16	*P. sinuatus*	Female	8,003	361	264	42	1
14-Dec-16	16-Dec-16	*P. sinuatus*	Female	5,800	315	237	72	2
14-Nov-17	05-Dec-17	*P. galeata*	Female	2,070	244	188	240	21
14-Nov-17	20-Nov-17	*P. galeata*	Female	980	207	165	75	6
15-Nov-17	24-Nov-17	*P. galeata*	Male	2,130	251	183	98	9
23-Jan-18	18-Jul-18	*P. galeata*	Male	1,420	208	153	2087	176
24-Jan-18	04-Mar-18	*P. galeata*	Female	2,580	251	188	457	39
25-Jan-18	21-Feb-18	*P. galeata*	Male	1,660	215	167	327	27
28-Jan-18	29-Jan-18	*P. galeata*	Female	1,740	221	170	14	1
29-Jan-18	27-Mar-18	*P. galeata*	Male	2,570	254	194	676	57
Ndumo total fixes and days data retrieved							2,238	105
Tala total fixes and days data retrieved							3,974	306

fyke nets at all sites. These nets (23 mm mesh) consisted of a single central leader (7–7.5 m long) with three internal valves and an opening height of 60–70 cm (T&L Netmaking, Mooroolbark, Australia). Both wire mesh traps and fyke nets were placed in relatively shallow water at each of the study sites, sitting on the ground and stabilized with metal rods, to prevent any chance of drowning individual terrapins. Both traps and nets were baited in the early mornings with 400 g of chicken liver and rebaited when necessary. We examined nets in the late afternoon on the day of the installment. After that, we examined them in the early mornings and late afternoon during their installed days.

Individual terrapins were permanently marked using a modified terrapin marking system (Cagle 1939, Price et al., 2021). Small drill holes were made, on the periphery scutes above the hindlegs. This gave a unique and recognizable identification if the individual was recaptured (Price et al., 2021).

We recorded the site's geographic location coordinates for each terrapin captured with a global positioning system (GPS) Garmin Etrex 100 (Garmin, Olathe, USA). The morphometrics we measured included the straight-line carapace length (SCL) and straight-line carapace width (SCW) to the nearest mm. These we measured using a large caliper (Haglof, S-882 00. Sweden) (Price et al., 2021). The total body mass of each to the nearest Gram was determined using a pre-weighed sack, using a hanging scale (Marco Portable Bag Scale – Black, UK). Juveniles were defined as individuals under 150 mm in SCL for *P. sinuatus* while under 120 mm for *P. galeata* (Price et al., 2021).

Tags were only attached to adult individuals. Terrapin sex was determined using external secondary sexual characteristics following Boycott and Bourquin (2000). We showed other terrapin experts the photographs to confirm the sex of the terrapins caught. We fitted tags and obtained stored and transmitted data from eight *P. sinuatus* (seven females and one male) and eight *P. galeata* (four males and four females; Table 1). After collecting morphological data and tagging, we released all terrapins at their capture site. We handled all terrapins for the minimum necessary time and per the herpetological animal care and use committee 2004 (Herpetological Animal Care Use Committee, 2004).

Radio-telemetry methods

We selected Ultra-High Frequency (UHF) radio telemeter tags (~22 g; less than 1% body mass of terrapins) adapted from fish telemeter tags for the present study (Wireless Wildlife, Potchefstroom, and Animal Trackem Ltd, Pietermaritzburg). We chose these for their small size, remote capabilities and ability to function in terrestrial and aquatic environments (Burnett et al., 2020). These telemeter tags had two sensors, an activity, and a temperature sensor, as per Burnett et al. (2020). The activity sensor recorded fine-scale temporal activity as activity counts per 1-h or 2-h interval, which was converted to an average activity count per minute. Consequently, we could detect inactivity and activity periods based on the number of counts over the stipulated time frame (1-h or 2-h schedule for this study) (Burnett et al., 2020). The tag schedules were set for a 1-h interval in Ndumo and changed to a 2-h interval in Tala. The difference in schedule was because of the need to extend the telemeter tags' battery life by recording data over a time interval that could still give reliable data. To analyze, when extended periods of inactivity occurred, we separated the data into inactive and active datasets, where inactive data were activity readings of less than one average activity count per minute. The active data activity readings were between 1 and 5,000 activity counts per minute. Telemeter tags recorded the ambient temperature and water temperature directly surrounding the carapace, defined as tag temperature depending on what environment the terrapin was in at the time. Further general temperature data were also retrieved from weather stations and defined as ambient temperature.

We established a remote network of receiver stations around Nyamithi Pan, Ndumo (Figure 1), and around sites in Tala (Figure 2). Tagged terrapins were detected at the nearest receiver station. The receiver stations received stored and real-time data from telemeter tags and then transferred the data to a central data management system remotely (Burnett et al., 2020). The remote networks could detect tagged terrapins in water within a 500 m range and outside of water up to 5 km in line of sight. This feature facilitated data collection from tagged terrapins in the range of the network remotely and played an important role in accessing data during the wet season at Ndumo when Nyamithi's Pan became inaccessible. Due to the multiple receiver stations, we attempted triangulation in the early stages of the research, but triangulation was inaccurate as data came to different stations at different times. Data were stored on the tag when out of range of receivers, and schedule changes could be made to track tags manually. On two occasions out of range, *P. sinuatus* individuals were manually tracked to locate their position outside the network coverage but were unsuccessful because of the site's remoteness.

Environmental variables

For the environmental factors, we used hourly data of atmospheric temperature (°C), wind (km/h) and rainfall (mm) from the two nearest South African Weather Service (SAWS) weather stations to the tagging locations. These environmental factors are known to affect the behavior and activity of terrapins (Bowen et al., 2005; Howard et al., 2017) and were available to determine the effects of these in the context of the present study. The weather station nearest Ndumo was Mbazwana Airfield (27°28′37.20″S 32°35′52.80″E), a straight-line distance of 70 km and within the same habitat type and eco-region as Ndumo. Although Tembe Elephant Park had a weather station closer to Ndumo, it was deemed unreliable as it was placed beside a helicopter pad and was missing data because of malfunction (pers. comm. C. Hanekom, district ecologist, Tembe Elephant Park). The weather station nearest Tala was a straight-line distance of 25 km from Tala (29° 37.620′S 30° 24.120′E) and within the same eco-region.

Data Analyses

The presence and locomotive activity data from the tags on terrapins were obtained from the central data management system. We analyzed the activity data using Microsoft (MS) Excel (©2017, Microsoft Corporation) and R 3.6.1 (R Core Team, 2017) with the added package Ime4 (Bates et al., 2014b). We separated the terrapins' activities into two classes because of their extended periods of inactivity when basking or resting (Rheingantz et al., 2016). These classes of "inactivity" and "activity" for each of the two species were then analyzed separately. Generalized linear mixed effects models (GLMM) were constructed using all possible combinations available and then selected to determine the relationship between environmental variables (obtained hourly from the respective SAWS weather stations) and terrapin activity data for each species. We tested for multicollinearity using the Pearson's test; models with scores lower than 0.6 were selected (Graham, 2003). Statistical outputs included residual degrees of freedom (df. res), log-likelihood (logLik) and delta Akaike Information Criterion (dAIC). Models were then formulated and selected based on dAIC values, standardized residuals and observed versus predicted values to find the most parsimonious model for interpretation (Akaike, 1973; Burnham and Anderson, 2002). Models were ranked and selected on the minimum dAIC value where dAIC values ≤2 provided evidence for the use of the model and used to explain the locomotive activity behavior of both *P. sinuatus* and *P. galeata* (Burnham and Anderson, 2002). The best fitted model was then used to determine the linear regression for tag temperature, wind and rainfall and the significance using the p-value ($p < 0.05$).

Results

The terrapins with telemeter tags showed site fidelity for their respective water bodies when conditions were relatively normal, that is, not in extreme drought or flooding conditions. Telemeter tags on terrapins in Ndumo transmitted data until the first heavy rains in Ndumo, showing the individual terrapins continued occupancy. In late December 2016 and early January 2017, Ndumo had its heaviest rains in over 2 years (pers. comm. C. Hanekom, district ecologist, Tembe Elephant Park). This created flooding, and a significant influx of water flowed through Nyamithi Pan into either the Phongola or Usuthu Rivers. Following this, all terrapins moved out of range of the established remote network and were not detected again. Several manual tracking attempts were made over 2 weeks after the tagged terrapins moved out of the remote network to relocate them. Terrapins did not move back in range of the remote network, which was left in place after the flood receded and tag battery life had ceased (after 12–

14 months), meaning none of the tagged animals returned within a year of the terrapins moving out of range.

At Tala, there was no such major shift in wetland/impoundment size despite summer rainfall, and no flooding occurred (pers. comm. Tala Management). Individuals typically stayed within range of the remote network. Still, if they were giving locomotive activity recordings of zero over an extended period (longer than 4 days), it was assumed the individuals either died or that the tags had dropped off prematurely.

The tag attachment test showed that the dummy tag remained on the *P. galeata* individual at the Animal House, University of KwaZulu-Natal, Pietermaritzburg, for 14 months. The individual did not appear to alter its behavior during this time. The dummy tag eventually fell off the carapace once the cable ties had degraded.

Only *P. galeata* was present in Tala, while the number of *P. galeata* in Ndumo was insufficient to obtain adequate samples sizes; therefore, only *P. sinuatus* were tagged in Ndumo. Adult female *P. sinuatus* are significantly heavier than the males (Price et al., 2021; Table 1). In comparison, adult *P. galeata* males and females have similar body mass (Price et al., 2021, Table 1).

Of the *P. galeata* and *P. sinuatus* terrapins tagged, 16 provided enough data to be used for data analyses, eight from each population. Due to the low number of data points with zero activity counts found for *P. sinuatus* in Ndumo, tags for Tala on *P. galeata* were set to a 2-h time interval to conserve battery life and increase tracking days for tagged individuals. This schedule change could still detect similar trends in behavioral data for *P. galeata*. We found a bimodal distribution for both species with distinct inactive and active periods (Figure 3). Periods of inactivity were shown to occur through the 24-h period; however, they occurred more frequently during the night rather than daylight periods for both species, showing both species are diurnal.

Male and female diurnal behavior were similar for each species (Figures 4 and 5). For *P. sinuatus,* only one male was tagged, resulting in low confidence; however, it showed high variability in its temporal activity compared with the females. Results from *P. galeata* showed females having less overall activity than males (Figures 4 and 5).

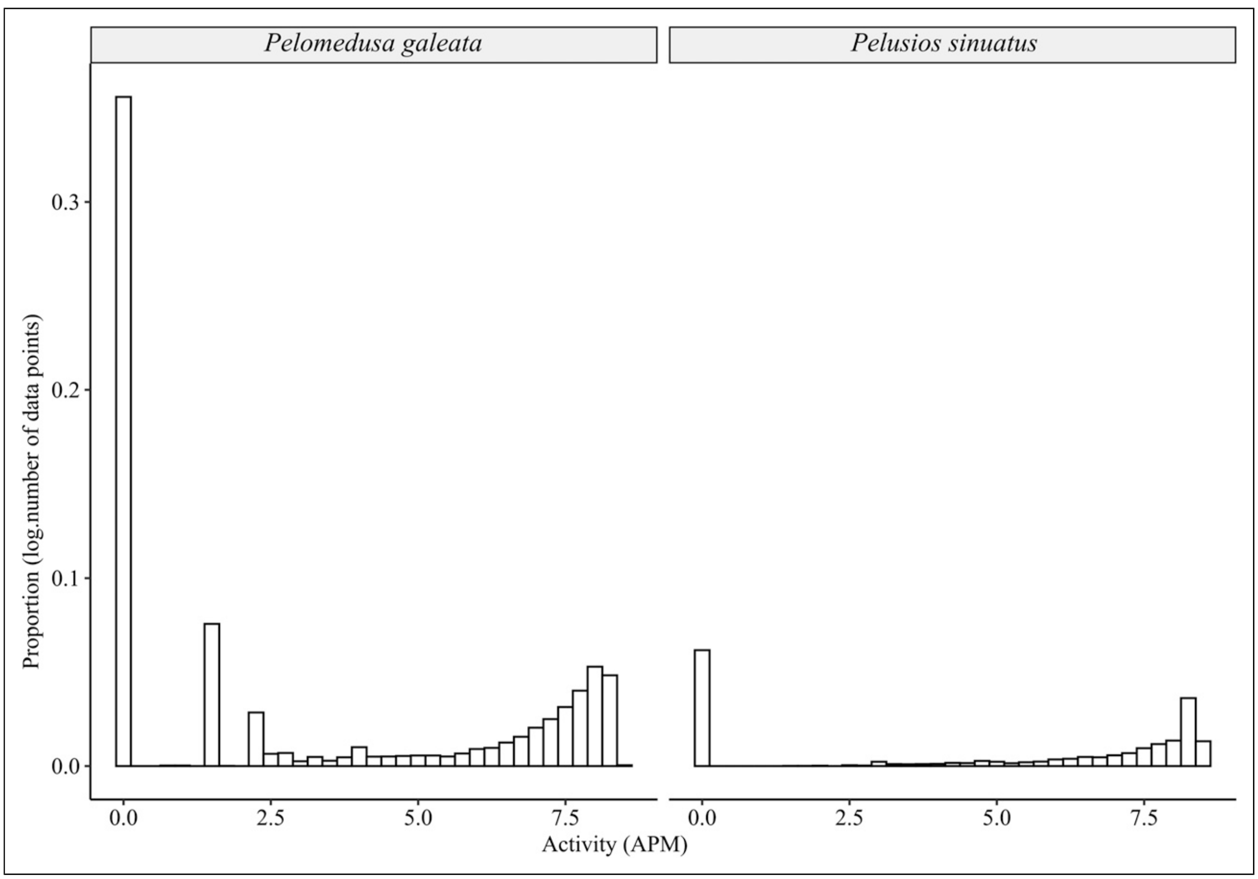

Figure 3. Bimodal frequency distribution of activity count data for *Pelomedusa galeata* and *Pelusios sinuatus,* indicating the high prevalence of inactive periods compared with active periods in the present study.

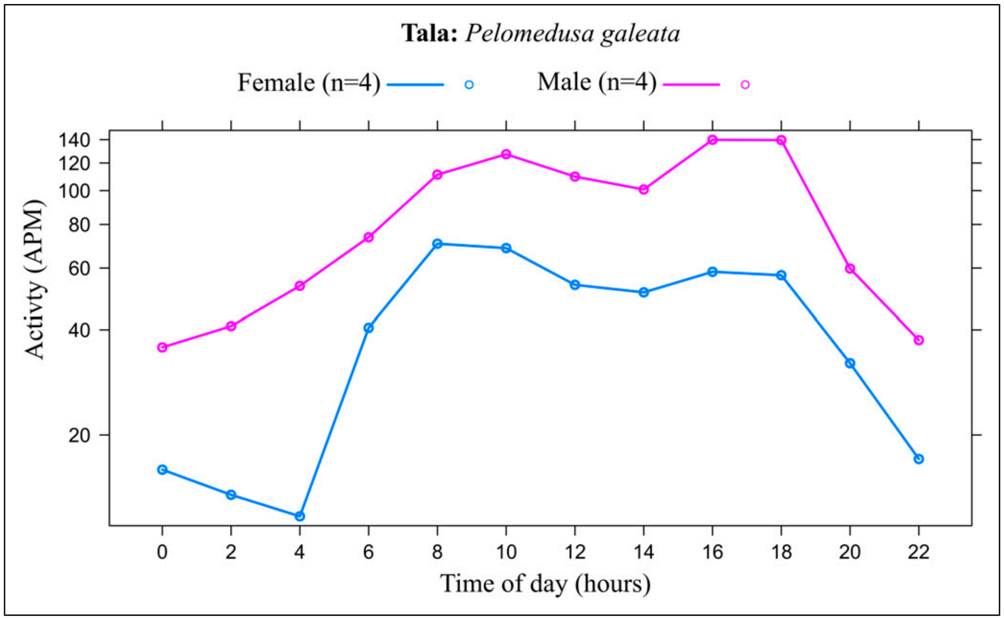

Figure 4. Diurnal behavior of male and female *Pelomedusa galeata* for each hour in the 24 h period. (Note: APM = average activity counts per min.).

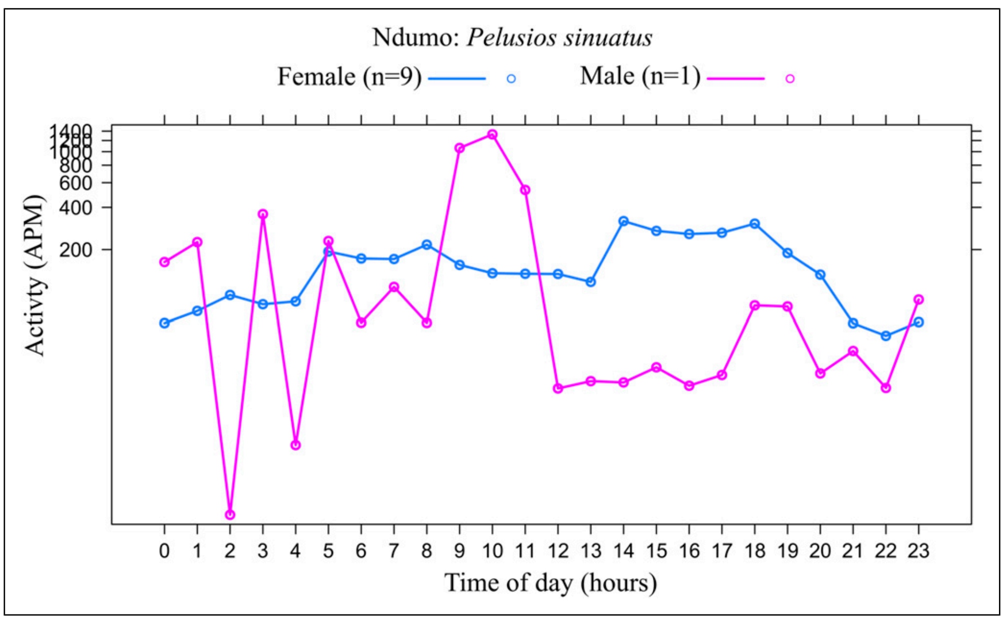

Figure 5. Diurnal behavior of male and female *Pelusios sinuatus* for each hour in the 24 h period. (Note: APM = average activity counts per min.).

The active dataset further showed diurnal activity patterns for both species, with reduced activity at night in conjunction with both tag temperature and ambient temperature recordings in a 24 h period (Figure 6). Tag temperature showed different temperature tolerance ranges for the two species, with *P. galeata* being active in cooler temperatures than *P. sinuatus* (Figure 6). Both species could manipulate their respective tag temperatures associated with their microhabitat preferences above the ambient temperatures at night. During the day, tag temperature was either matching or below the average ambient temperatures (Figure 6; Tables 2, 3, and 4). In the cooler parts of the day, from midnight to 10h00, *P. galeata* tag temperatures were above that of ambient temperatures (Figure 7; Table 3).

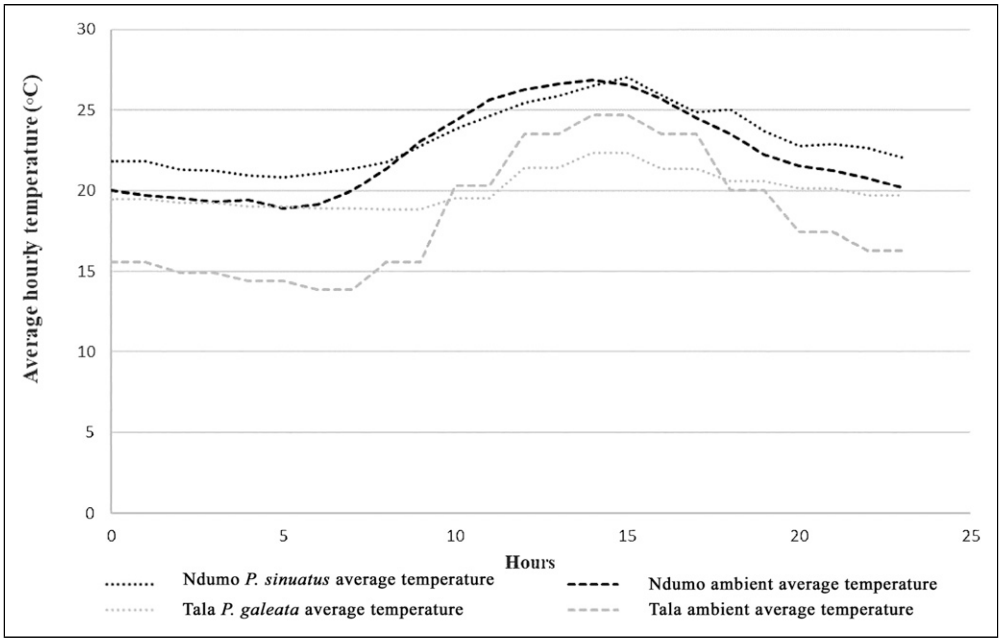

Figure 6. Average ambient temperature (Ta) ranges for the study sites Ndumo Game Reserve and Tala Private Reserve, and average tag temperature (Tt) ranges for *Pelusios sinuatus* and *Pelomedusa galeata,* respectively, over a 24-h period during the study. (Note: *P. galeata*'s ability in the first 10 h period of a day to maintain a Tt ~ 5°C above Ta).

Table 2. Daily hourly mean tag temperature (Tt) and ambient temperature (Ta) for *Pelusios sinuatus* (*n* = 8) at Ndumo Game Reserve in the present study from August 2016 until December 2016.

TOD	Mean Tt (oC)	±SD.	Max	Min	Mean Ta (oC)	±SD.	Max	Min
1	21.8	3.3	27.5	10.9	20.0	2.7	24.1	10.5
2	21.8	2.8	27.0	15.4	19.7	2.7	24.0	9.8
3	21.3	3.3	26.8	6.7	19.6	2.8	23.4	9.8
4	21.2	3.2	26.6	9.4	19.3	2.8	23.3	10.3
5	21.0	3.4	26.3	4.4	19.4	2.8	23.3	10.1
6	20.8	2.8	26.0	11.6	18.9	3.1	23.0	7.8
7	21.1	2.8	26.2	13.7	19.1	3.2	23.3	7.8
8	21.3	3.1	26.1	10.7	20.0	3.3	25.4	8.4
9	21.8	3.3	30.4	14.5	21.4	3.5	28.6	10.6
10	22.8	3.3	27.7	14.6	23.1	3.1	28.8	14.8
11	23.8	3.6	38.1	15.6	24.4	2.8	31.5	17.0
12	24.7	3.8	35.0	12.6	25.6	3.1	34.9	20.3
13	25.4	3.8	36.5	15.4	26.3	3.4	36.2	20.6
14	25.9	3.7	35.1	18.6	26.6	3.4	36.2	20.5
15	26.5	4.5	38.9	15.2	26.9	3.6	35.1	18.9
16	27.0	4.5	43.9	13.3	26.6	3.7	38.2	18.9
17	25.9	4.1	35.6	14.9	25.7	3.4	35.0	18.4
18	24.9	4.1	34.2	11.1	24.5	2.7	30.6	17.5
19	25.1	3.3	32.8	17.4	23.5	2.5	28.6	15.4
20	23.7	3.1	29.3	16.1	22.2	2.4	27.7	15.1
21	22.7	3.3	28.6	12.7	21.5	2.3	27.0	13.9
22	22.9	3.0	28.1	13.9	21.2	2.4	24.8	13.4
23	22.7	2.7	27.7	16.3	20.8	2.7	24.5	13.3
24	22.0	3.2	27.6	9.4	20.2	2.7	24.2	13.3

At both study sites, the GLMM's most significant environmental variable that affected both terrapin species' temporal activity was the ambient temperature ($p < 0.001$), followed by rainfall ($p < 0.05$), which had a less obvious effect but still a significant effect (Figures 7 and 8, Tables 2 and 3). Wind showed no significant effect.

Discussion

The field application of the telemeter tags on terrapins in this study was important in understanding the effects of drought and subsequent flooding at Ndumo and the availability of suitable habitat in Tala's impoundments. With increased erratic rainfall predicted for the region because of climate change (IPCC, 2021; Kusangaya et al., 2018), the flood events as documented in the present study could become more frequent and coupled by drier periods between rainfall events can further affect the persistence of terrapins in the region. Our results demonstrated the significant effect temperature and rainfall have on both species temporal activity and presence within an area. Most significantly, the sudden heavy rain and flooding caused *P. sinuatus* to be swept out of range of our remote network. In addition, the results demonstrated *P. galeata's* ability to maintain tag temperature above ambient temperature in the first 10-h period of a day. These findings were achieved by analyzing the tag data in conjunction with the environmental variables data retrieved from the weather stations. In addition, in the present study, drought caused the drying of wetlands and pans, causing terrapins to either move away, attempt a prolonged period of

Table 3. Daily two-hourly mean tag temperature (Tt) and ambient temperature (Ta) for *Pelomedusa galeata* (*n* = 8) at Tala Private Nature Reserve in the present study from November 2017 to July 2018.

TOD	Mean Tt (°C)	±SD.	Max	Min	Mean Ta (°C)	±SD.	Max	Min
2	19.5	3.65	25.4	7.2	15.5	4.19	22.5	3.2
4	19.3	3.67	25.2	9.4	14.9	4.20	22.1	1.6
6	19.0	3.74	25.1	7.9	14.4	4.46	23.5	1.4
8	18.9	3.72	25.2	7.9	13.8	4.63	21.9	0.7
10	18.9	3.80	25.1	6.4	15.6	5.69	26.8	2.9
12	19.6	4.02	40.8	5.9	20.3	4.79	31.8	10.0
14	21.4	4.22	37.4	5.8	23.5	4.63	34.5	11.2
16	22.3	4.40	41.6	5.9	24.7	4.70	35.2	10.0
18	21.4	4.18	37.6	5.1	23.5	4.53	35.5	7.9
20	20.6	3.73	28.17	4.9	20.0	3.91	31.5	8.5
22	20.1	3.72	27.0	3.7	17.4	3.65	29.3	6.1
24	19.7	3.64	25.5	8.6	16.3	4.00	23.7	4.7

Table 4. Summary of the top GLMM's with random effects showing the effect of environmental variables on the activity of *Pelomedusa galeata* and *Pelusios sinuatus*. (Note: DF = degrees of freedom, LogLik = the logged likeliness; dAIC = the delta Akaike's information criteria).

Species	Selected model	DF residual	LogLik	dAIC
Pelomedusa galeata	Activity rates ~Temperature+Rain	226	37.779	0
	Activity rates ~Temperature+Rain+Wind speed	225	36.360	0.6
Pelusios sinuatus	Activity rates ~Rain	103	16.910	0
	Activity rates ~Temperature+Rain	102	16.992	1.9
	Activity rates ~Rain+Wind speed	102	16.804	2

estivation, or greatly reduce temporal activity (Price et al., 2021). These results are even more concerning when considering southern Africa's (IPCC, 2021) predictions.

The Australian freshwater turtle, *Chelodina longicollis*, similarly responded to low water levels during drought by moving and, in this case, into sheltered woodland microhabitats and estivating there for several months (Rees et al., 2009). In addition, during drought, these terrapins were less abundant and grew slower (Ferronato et al., 2017). Since our receivers were kept in place and the tag battery life was for 12–14 months, we concluded that none of the eight *P. sinuatus* tagged individuals returned to Nyamithi Pan following the flooding.

Monitoring the continued presence and temporal activity patterns of small semi-aquatic animals using telemeters highlights the value of these telemeters and the remote network of receiver stations as a conservation monitoring tool. Generally, this has been a significant challenge because of technological limitations. These limitations are even further apparent in remote and challenging field sites, such as Ndumo, or when data must be retrieved over a considerable length of time. Unfortunately, determining the exact locality and spatial movement of terrapins requires the use of GPS tags as our data could not triangulate each terrapin's position. However, data showed terrapin site fidelity for when conditions were suitable.

Our tag retention test findings aided in the unwasted expenditure on costly tags purchased abroad, often limiting telemetry research in developing countries (Burnett et al., 2021). The cable ties secured the telemeter tag well beyond its life span (1 year). The dislodging from the terrapin freed it of the telemeter tag. Little hindrance of the tagged terrapin behavior relative to the untagged terrapins showed that the telemeter tag could be used in field applications without significantly altering tagged individuals' behavior. The success of the pilot study was valuable for the field application.

As our results demonstrated, less predictable and above and below usual temperatures will negatively affect terrapin temporal activity. Furthermore, the concurrent research showed a skewed size class bias towards adult individuals throughout the province, with relatively few juveniles (Price et al., 2021). This appears likely because of unfavorable conditions for juveniles, with the larger, more resilient adults able to persist.

A limitation of the telemeter tags was the inability to account for if the animal had died or whether the tag had dropped off or malfunctioned, as found in other studies (Klinard and Matley, 2020). These limitations were overcome by thoroughly examining the data and closely examining the temperature data against the weather station data. The tag's battery life (minimum 1 year) could account for any animal(s) attempted estivation. As previously discussed, we reduced the risk of the tags dropping off to an absolute minimum with our animal house dummy tag test. Two of the tags for both species were removed from analyses where the tag data was deemed unreliable. In the present study, individual terrapins that had zero locomotive activity for an extended period (longer than 4 days, when environmental variables indicated good conditions for activity) were assumed to have either died or that the tags had dropped off prematurely, as in other studies (Klinard and Matley, 2020), or to have moved out of the network range. During periods of rain, *P. galeata* is known to transverse distances over land, with records of individuals traveling over 5 km (Stuart and Meakin, 1983; Vamberger et al., 2019a), and the individuals at Tala likely went out of range of the network.

For both terrapin species, the telemeter tags successfully determined the fine-scale temporal activity of individuals. The data obtained showed that both species were diurnal and had extended periods of inactivity at night. The latter had not

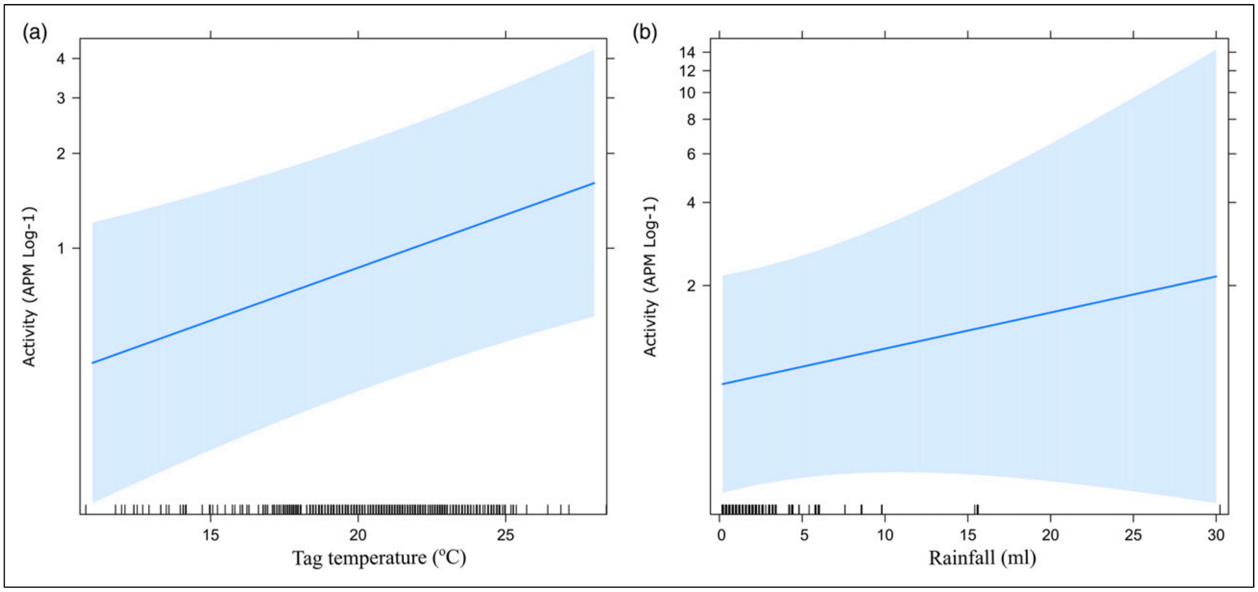

Figure 7. Generalized linear modeling results indicating significant effects of tag temperature (A) and rainfall (B) on the activity of *Pelusios sinuatus* at Ndumo Game Reserve.

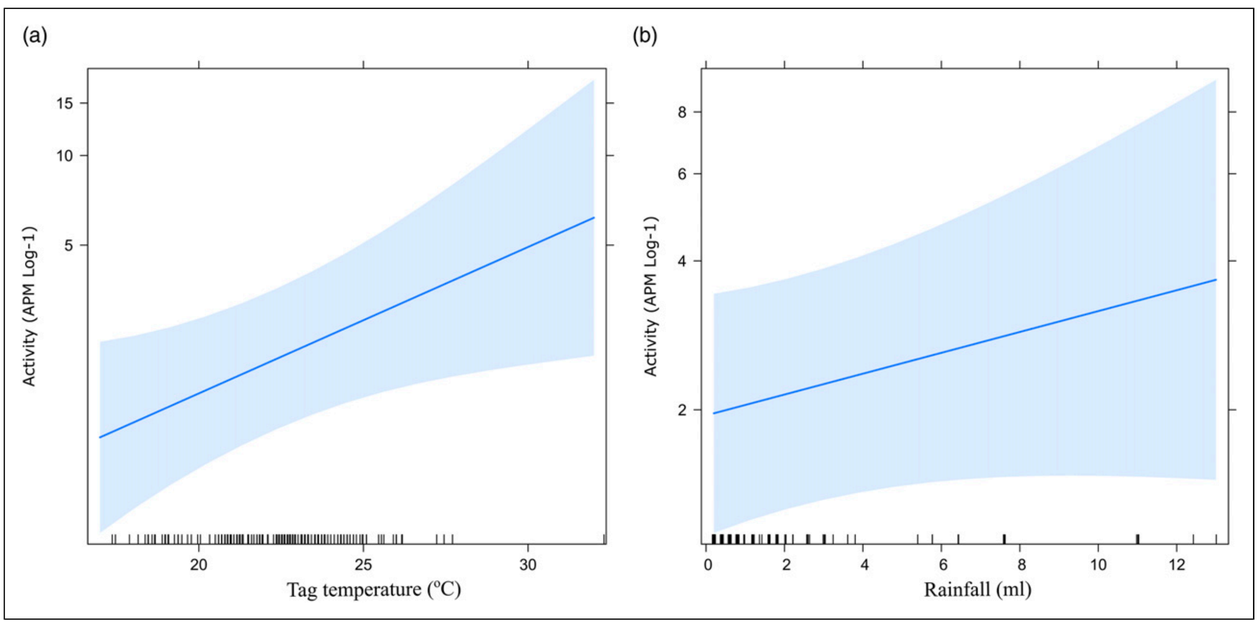

Figure 8. Generalized linear modeling results indicating significant effects of (A) tag temperature and (B) rainfall on the activity of *Pelomedusa galeata* at Tala Private Nature Reserve.

previously been recorded. Similar diurnal activity patterns were found for leopard tortoises (*Stigmochelys pardalis*) in southern Africa (McMaster and Downs, 2013).

Research into temporal activity budgets of terrapins generally has been constrained by the size and cost of telemetry equipment, as well as its efficiency and, in many cases, the rapidly changing dynamic habitats in which these species reside (Luiselli, 2008; Roe and Georges, 2008; Thomas et al., 2011). Early radio-telemetry research raised concerns about the impact on turtle and terrapin behavior because of the relatively large transmitter size and drag potential for aquatic species. This generally included far larger species such as the marine turtles and other semi-aquatic reptiles such as Nile crocodiles (*Crocodylus niloticus*) (Watson and Granger, 1998; Calverley and Downs, 2015; Combrink et al., 2017). As in the present study, recent developments have overcome these concerns with smaller transmitters with longer transmission range and life spans

(Gibbons and Lovich, 2019; Burnett et al., 2020). As with Ndumo in this study, research site access is still a challenge, as with many other remote sites in developing countries (Hocutt et al., 1994). These limitations have resulted in Africa's freshwater aquatic species being relatively poorly studied, but with innovative telemetry solutions developed to overcome these in southern Africa, this is now changing (Burnett et al., 2020; Burnett et al., 2021). These features assist in effectively using aquatic telemetry on these semi-aquatic species, particularly given their remote capabilities. Telemetry tag size in relation to body mass is becoming less of an obstacle as technological advances continue. This enables researchers to focus on smaller species to conduct long-term, remote telemetry research important for ecological studies (Roe and Georges, 2008; Doody et al., 2009; Howard et al., 2017).

At both study areas in the present study, the most significant climatic variables that affected both terrapin species' activity were ambient temperature and rainfall, while wind showed no significant effect. These two climatic variables will continue to become more erratic and difficult to predict in the future (IPCC, 2021). Individuals of *P. galeata* showed a greater ability to maintain carapace temperature above ambient temperature in the first 10 h of a day than *P. sinuatus*. This is probably more necessary for *P. galeata* to attain because of Tala's eco-region, being "southeastern uplands," compared with Ndumo with warmer sub-tropical temperatures (Whittington et al., 2013; Humphries et al., 2016). Both species' ability (particularly *P. galeata*) to maintain a carapace temperature above that of the recorded ambient temperatures was novel and noteworthy considering their conservation into the future. This is probably achieved via micro-habitat use, showing the importance of high diversity and functioning wetland habitats for the species. Reptiles are ectothermic, and so their activity and movements are particularly affected by climatic variables and their ability to regulate body temperature behaviorally and sustain biological functions, such as egg development (Carrière et al., 2008; Ihlow et al., 2012; McMaster and Downs, 2013). Less predictable and more erratic weather/environmental patterns because of climate change will bring further challenges to terrapins (Bombi et al., 2009). Understanding how these species respond to environmental changes is important when assessing the effects of future climate change scenarios. Our baseline data demonstrates how our tagged individuals' tag temperatures differed from the surrounding ambient temperature recordings at times, thus demonstrating their thermoregulation abilities and finding more suitable microhabitats.

Semi-aquatic ectothermic species like terrapins face the thermal complexity of transitioning between a relatively stable thermal environment (water) into one characterized by short term temperature fluctuations (atmosphere) on a constant and regular basis (Miller, 1979). Of the vertebrate species that inhabit riverine systems, terrapins semi-aquatic behavior and life-history traits make them important for understanding the link between aquatic and terrestrial habitats (Bodie and Semlitsch 2000). For the most effective protection of any species, understanding their behavior is essential (Cooke et al., 2013). As semi-aquatic species, it is difficult to estimate the species locomotive activity and spatial ecology because of the dynamic and sometimes dramatic fluctuations of wetlands in terms of size and habitat variability (Ferronato et al., 2017; Grundling et al., 2013). The fluctuations of the wetland habitat can drive semi-aquatic species to change general activity and movement. Reptiles are often undervalued or under-studied in freshwater systems despite the important link they have between terrestrial and aquatic ecosystems (Doody et al., 2009; Sterrett et al., 2015).

The success in tag attachment, both in the field and laboratory, and the remote telemetry receiver network setup still presented some technological limitations in this study. Further research design can improve these. One such improvement is the use and incorporation of a GPS sensor. Furthermore, the present study demonstrated the importance of local development and production of telemetry techniques (tags, receivers, and support) in South Africa. This allowed for a more affordable option and specific development of telemetry technology to address how aquatic and semi-aquatic species respond to local water resource issues (Dube et al., 2015; Burnett et al., 2021). This approach's development will assist with telemetry projects on terrapin species within Africa and reduce unforeseen costs and complications that may incur in methods in the future.

In conclusion, this telemetry technique's major benefits were the remote aspect. This allowed for hourly or once every 2 hours data to be collected, stored, and eventually remotely sent to researchers, of two small cryptic, semi-aquatic species, in difficult to access field sites. This enabled valuable insights into both species' continued presence and locomotive behavior in relation to environmental/climatic variables. More importantly, the data helps further understand the behavioral responses of terrapins to environmental and climatic changes. "To establish whether, in fact, Cape terrapins do move away from dry water bodies into open country during dry spells would require the implementation of a radio-telemetry programme." (Stuart and Meakin, 1983). Despite this statement almost 40 years ago, no wild terrapins in southern Africa had been the focus of telemetry research until the present study. Telemetry technology has made great strides and continues to do so. We encourage a further focus on telemetry methods for terrapins in Africa to understand their response to increased droughts with anthropogenic climate change.

Implications for Conservation

One of the main threats to terrapin populations viability is their reliance on ponds and wetland habitat being connected. Loss of connectivity of wetland habitat can be detrimental to terrapins by increasing the chances of local extinctions and reducing re-colonization opportunities (Serrano et al., 2020). Of the 105 species of Chelonian currently listed as data deficient, not listed, or not evaluated by the IUCN, 31% are found in Africa (Luiselli et al., 2021). Our own targeted species, the serrated hinged terrapin, falls within this category of not evaluated, whereas the marsh terrapin is considered least concern, the methods implemented in our research can be repeated and replicated to do further long-term remote monitoring of more threatened species of terrapin, particularly in West Africa (Luiselli et al., 2021). The present study highlights the need to collect field data on movement and activity for generally overlooked small semi-aquatic species as a conservation priority for these taxa and their habitats. Monitoring the temporal activities compared with environmental variables can be replicated in remote and challenging field sites with our methods. We strongly encourage such research for other terrapin species throughout Africa.

Acknowledgments

We conducted all trapping and data collection on terrapins with permission from Ezemvelo KZN Wildlife. All the staff at Tala Private Game Reserve and Ndumo Game Reserve are thanked for their support. F. Botha (Wireless Wildlife Ltd) and V. Hugo (Animal Track-em Ltd) are thanked for designing and manufacturing the tag units and their ongoing technical support and guidance throughout the research. The Ford Wildlife Foundation (ZA) is thanked for providing a 4x4 vehicle for this research. The South African Weather Service (SAWS) kindly provided the requested weather data. Raw data are available upon request to the corresponding author(s). We are grateful for the constructive comments of the reviewers and editor that improved the manuscript.

Declaration of Conflicting Interests

The author(s) declare no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was supported by the National Research Foundation (ZA, Grant 98404), the University of KwaZulu-Natal (ZA) and the Ford Wildlife Foundation (ZA) are thanked for their support.

Research ethics

We conducted all trapping and data collection on terrapins with permission from Ezemvelo KZN Wildlife (permit number OP 2296/2016) and ethical approval from the University of KwaZulu-Natal Animal Ethics subcommittee (Reference number: 020/15/Animal).

ORCID iDs

Cormac Price https://orcid.org/0000-0002-9092-0796
Matthew J Burnett https://orcid.org/0000-0002-6237-1697
Gordon O'Brien https://orcid.org/0000-0001-6273-1288
Colleen T Downs http://orcid.org/0000-0001-8334-1510

References

Abbas, H. A., Bond, W. J., & Midgley, J. J. (2019). The worst drought in 50 years in a South African savannah: Limited impact on vegetation. *Afr J Ecol*, *57*(4), 490-499. https://doi.org/10.1111/aje.12640.

Akaike, H. (1973). Information theory and an extension of maximum likelihood principle. In B. N Petrov, & F Csaki (Eds), *Second International Symposium on Information Theory*. Budapest: Akademiai Kiado. 267–281).

Basile, ER, Avery, HW, Bien, WF, et al. (2011). Diamondback terrapins as indicator species of persistent organic pollutants: Using Barnegat Bay, New Jersey as a case study. *Chemosphere*, *82*(1), 137-144. https://doi.org/10.1016/j.chemosphere.2010.09.009.

Bates, M. F., Branch, W., Bauer, A., et al (2014a). Atlas and red list of the reptiles of South Africa. *Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.

Bates, D., Maechler, M., Bolker, B., et al. (2014b). linear mixed-effects models using Eigen and S4. Retrieved From: October 2019, http://cran.r-projectorg/package=lme4

Bodie, JR, & Semlitsch, RD (2000). Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia*, *122*(1), 138-146. https://doi.org/10.1007/PL00008830.

Bombi, P., D'Amen, M., Gerlach, J., et al (2009). Will climate change affect terrapin (*Pelusios subniger paritalis* and *P. castanoides intergularis*) conservation in Seychelles. *Phelsuma*, *17*(A), 1–12. https://islandbiodiversity.com/Phelsuma17A1.pdf.

Bowen, K. D., Spencer, R. J., & Janzen, F. J. (2005). A comparative study of environmental factors that affect nesting in Australian and North American freshwater turtles. *J Zoolog*, *267*(4), 397-404. https://doi.org/10.1017/S0952836905007533.

Boycott, R. C, & Bourquin, O. (2000). The southern African Tortoise Book A guide to southern African Tortoises, Terrapins and Turtles. Pietermaritzburg, South Africa: Interpak.

Burnham, K. P., & Anderson, D. R (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. USA: Springer. p 488

Burnett, M. J., O'Brien, G. C., Jacobs, F., et al. (2020). The southern African inland fish tracking programme (FISHTRAC): An evaluation of the approach for monitoring ecological consequences of multiple water resource stressors, remotely and in real-time. *Ecol Indicators*, *111*(106001). https://doi.org/10.1016/j.ecolind.2019.106001.

Burnett, M. J., O'Brien, G. C., Jacobs, F. J., et al. (2021). Fish telemetry in African inland waters and its use in management: a review. *Rev Fish Biol Fish*, *31*(2), 337-357. https://doi.org/10.1007/s11160-021-09650-2.

Cagle, F. R. (1939). A System of marking turtles for future identification. *Copeia*, *1939*(3), 170-173. https://doi.org/10.2307/1436818.

Calverley, P. M., & Downs, C. T. (2014). T. Habitat use by Nile Crocodiles in Ndumo Game Reserve, South Africa: A naturally patchy environment. *Herpetologica*, *70*(4), 426-438. https://doi.org/10.1655/HERPETOLOGICA-D-13-00088.

Calverley, P. M., & Downs, C. T (2015). Movement and home range of Nile Crocodiles in Ndumo Game Reserve, South Africa. *Koedoe*, *57*, 1-13. http://doi.org/10.4102/KOEDOE.V57I1.1234.

Carrière, M.-A., Rollinson, N., Suley, A. N., et al. (2008). Thermoregulation when the growing season is short: sex-biased basking patterns in a northern population of painted turtles (*Chrysemys Picta*). *J Herpetology*, *42*(1), 206-209. https://doi.org/10.1670/07-070R1.1.

Chessman, B. C. (2019). Behavioural thermoregulation by Australian freshwater turtles: interspecific differences and implications for responses to climate change. *Aust J Zoolog*, *67*(2), 94-105. https://doi.org/10.1071/ZO20004.

Combrink, X, Warner, JK, & Downs, CT (2017). Nest-site selection, nesting behaviour and spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. *Behav Process*, *135*, 101-112. https://doi.org/10.1016/j.beproc.2016.12.006.

Cooke, S. J., Midwood, J. D., Thiem, J. D., et al. (2013). Tracking animals in freshwater with electronic tags: past, present and future. *Anim Biotelemetry*, *1*(5). https://doi.org/10.1186/2050-3385-1-5.

Dalhuijsen, K., Branch, W. R., & Alexander, G. J. (2014). A comparative analysis of the diets of *Varanus albigularis* and *Varanus niloticus* in South Africa. *Afr Zoolog*, *49*(1), 83-93. https://doi.org/10.1080/15627020.2014.11407621.

Doody, J. S., Roe, J., Mayes, P., et al. (2009). Telemetry tagging methods for some freshwater reptiles. *Mar Freshw Res*, *60*(4), 293-298. https://doi.org/10.1071/MF08158.

Dube, T., Mutanga, O., Seutloali, K., et al. (2015). Water quality monitoring in sub-Saharan African lakes: a review of remote sensing applications. *Afr J Aquat Sci*, *40*(1), 1-7. https://doi.org/10.2989/16085914.2015.1014994.

Fairbanks, D. H. K., & Benn, G. A. (2000). Identifying regional landscapes for conservation planning: a case study from KwaZulu-Natal, South Africa. *Landscape Urban Plann*, *50*(4), 237-257. https://doi.org/10.1016/S0169-2046(00)00068-2.

Famelli, S., Souza, F. L., Georges, A., et al. (2016). Movement patterns and activity of the Brazilian snake-necked turtle *Hydromedusa maximiliani* (Testudines: Chelidae) in southeastern Brazil. *Amphibia-Reptilia*, *37*(2), 215-228. https://doi.org/10.1163/15685381-00003047.

Ferronato, B. O., Roe, J. H., & Georges, A. (2017). Responses of an Australian freshwater turtle to drought-flood cycles along a natural to urban gradient. *Austral Ecol*, *42*(4), 442-455. https://doi.org/10.1111/aec.12462.

Gibbons, J. W., & Lovich, J. E. (2019). Where has turtle ecology been, and where is it going? *Herpetologica*, *75*(1), 4-20. https://doi.org/10.1655/D-18-00054.

Graham, M. H (2003). Confronting multicollinearity in ecological multiple regression. *Ecol*, *84*, 2809-2815. https://doi.org/10.1890/02-3114.

Grundling, A. T., Van den Berg, E. C., & Price, J. S (2013). Assessing the distribution of wetlands over wet and dry periods and land-use change on the Maputaland Coastal Plain, north-eastern KwaZulu-Natal, South Africa. *South Afr J Geomatics*, *2*, 120–138. https://sajg.org.za/index.php/sajg/article/view/84.

Herpetological Animal Care Use Committee (2004). *Guidelines for use of live amphibians and reptiles in field and laboratory research* (2nd ed., p. 43). American Society of Ichthyologists and Herpetologists.

Hocutt, C., Seibold, S., & Jesien, R (1994). Potential use of biotelemetry in tropical continental waters. *Revue D'hydrobiologie Tropicale*, *27*, 77–95. https://core.ac.uk/download/pdf/39857219.pdf.

Howard, K., Beesley, L., Ward, K., et al. (2017). Preliminary evidence suggests freshwater turtles respond positively to an environmental water delivery during drought. *Aust J Zoolog*, *64*, 370-373. https://doi.org/10.1071/ZO16076.

Howell, H. J. Jr., Legere, R. H., Legere, R. H., etal. (2019). Long-term turtle declines: Protected is a verb, not an outcome. *Copeia*, *107*(3), 493-501. https://doi.org/10.1643/CH-19-177.

Humphries, B. D., Ramesh, T., Hill, T. R., et al. (2016). Habitat use and home range of black-backed jackals (*Canis mesomelas*) on farmlands in the Midlands of KwaZulu-Natal, South Africa. *Afr Zoolog*, *51*(1), 37-45. https://doi.org/10.1080/15627020.2015.1128356.

Hussey, NE, Kessel, ST, Aarestrup, K, et al. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, *348*(6240), 1255642. https://doi.org/10.1126/science.1255642.

Ihlow, F., Dambach, J., Engler, J. O., Rödder, D, et al. (2012). On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Glob Change Biol*, *18*, 1520-1530. https://doi.org/10.1111/j.1365-2486.2011.02623.x.

IPCC (2021). Climate Change 2021: The Physical Science Basis. *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, In V. P. Zhai, A. Pirani, et al (Eds)]. Cambridge: Cambridge University Press.

Iverson, JB (1982). Biomass in turtle populations: A neglected subject. *Oecologia*, *55*(1), 69-76. https://doi.org/10.1007/BF00386720.

Kimmons, J. B., & Moll, D. (2010). Seed dispersal by red-eared sliders (*Trachemys scripta elegans*) and common snapping turtles (*Chelydra serpentina*). *Chelonian Conservation Biol*, *9*(2), 289-294. https://doi.org/10.2744/CCB-0797.1.

Klinard, N. V., & Matley, J. K. (2020). Living until proven dead: addressing mortality in acoustic telemetry research. *Rev Fish Biol Fish*, *30*(3), 485-499. https://doi.org/10.1007/s11160-020-09613-z.

Kusangaya, S., Warburton Toucher, M. L., & van Garderen, E. A. (2018). Evaluation of uncertainty in capturing the spatial variability and magnitudes of extreme hydrological events for the uMngeni catchment, South Africa. *J Hydrol*, *557*, 931-946. https://doi.org/10.1016/j.jhydrol.2018.01.017.

Lovich, J. E., Ennen, J. R., Agha, M., et al. (2018). Where have all the turtles gone, and why does it matter? *BioScience*, *68*(10), 771-781. https://doi.org/10.1093/biosci/biy095.

Luiselli, L (2008). A model assessing the conservation threats to freshwater turtles of Sub-Saharan Africa predicts urgent need for continental conservation planning. *Biodiversity and Conservation*, *18*(1349). https://doi.org/10.1007/s10531-008-9486-1.

Luiselli, L., Diagne, T., & McGovern, P (2021). Prioritizing the next decade of freshwater turtle and tortoise conservation in West Africa, *Journal for Nature Conservation*. *60*, 125977. https://doi.org/10.1016/j.jnc.2021.125977.

McMaster, M. K., & Downs, C. T (2013). Seasonal and daily activity patterns of leopard tortoises (*Stigmochelys pardalis* Bell, 1828) on farmland in the Nama-Karoo, South Africa. *Afr Zoolog*, 48 72-83. https://doi.org/10.1080/15627020.2013.11407570.

Miller, D. G. M. (1979). Daily basking patterns of the freshwater turtle. *South Afr J Zoolog*, *14*(3), 139-142. https://doi.org/10.1080/02541858.1979.11447663.

Pérez-Pérez, A, López-Moreno, AE, Suárez-Rodríguez, O, et al. (2017). How far do adult turtles move? Home range and dispersal of *Kinosternon integrum*. *Ecol And Evol*, *7*, 8220-8231. https://doi.org/10.1002/ece3.3339.

Pooley, A. C (1982). The Ecology of the Nile Crocodile. *Crocodylus niloticus*, in Zululand. *MSc Thesis*. South Africa, Durban: University of Natal

Price, C., Hanzen, C., & Downs, C. T. (2021). Demographics and morphometrics of marsh terrapins (*Pelomedusa galeata*) and serrated hinged terrapins (*Pelusios sinuatus*) populations in KwaZulu-Natal, South Africa: skewed size-class bias concerns. *Zoomorphology*, *140*(2), 291-299. https://doi.org/10.1007/s00435-021-00518-4.

R Core Team (2017). A language and environment for statistical computing. Vienna: R foundation for Statistical Computing.

Rheingantz, M. L., Leuchtenberger, C., Zucco, C. A., et al. (2016). Differences in activity patterns of the Neotropical otter *Lontra longicaudis* between rivers of two Brazilian eco-regions. *J Trop Ecol*, *32*(2), 170-174. https://doi.org/10.1017/s0266467416000079.

Rees, M., Roe, J. H., & Georges, A. (2009). Life in the suburbs: Behavior and survival of a freshwater turtle in response to drought and urbanization. *Biol Conservation*, *142*(12), 3172-3181. https://doi.org/10.1016/j.biocon.2009.08.019.

Ríos-Saldaña, C. A., Delibes-Mateos, M., & Ferreira, C. C (2018). Are fieldwork studies being relegated to second place in conservation science? Global Ecology and Conservation, *14*, e00389. https://doi.org/10.1016/j.gecco.2018.e00389.

Rödel, M.-O. (1999). Predation on tadpoles by hatchlings of the freshwater turtle. *Amphibia-Reptilia*, *20*(2), 173-183. https://doi.org/10.1163/156853899X00187.

Rodell, M, Famiglietti, JS, Wiese, DN, et al. (2018). Emerging trends in global freshwater availability. *Nature*, *557*(7707), 651-659. https://doi.org/10.1038/s41586-018-0123-1.

Roe, J. H., & Georges, A. (2008). Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. *Austral Ecol*, *33*(8), 1045-1056. https://doi.org/10.1111/j.1442-9993.2008.01877.x.

Serrano, F., Pita, R., Mota-Ferreira, M., et al. (2020). Landscape connectivity affects individual survival in unstable patch networks: The case of a freshwater turtle inhabiting temporary ponds. *Freshw Biol*, *65*(3), 540-551. https://doi.org/10.1111/fwb.13449.

Sonamzi, B., Burnett, M., Petersen, R., et al. (2020). Assessing tagging and vulnerability to predation in tigerfish (*Hydrocynus vittatus*, Castelnau, 1861) in a water-stressed system using telemetry methods. *Koedoe*, *62*, a1649. https://doi.org/10.4102/koedoe.v62i1.1649.

Sterrett, S. C., Maerz, J. C., & Katz, R. A (2015). What can turtles teach us about the theory of ecological stoichiometry? *Freshw Biol 60, 443-455*. https://doi.org/10.1111/fwb.12516.

Stuart, C. L., & Meakin, P. R. (1983). Notes on the Cape Terrapin, *Pelomedusa subrufa* (Pleurodira: Pelomedusidae) in the Eastern Robertson Karoo. *J Herpetological Assoc Africa*, *29*(1), 9-11. https://doi.org/10.1080/04416651.1983.9650125.

Thomas, B., Holland, J. D., & Minot, E. O. (2011). Wildlife tracking technology options and cost considerations. *Wildl Res*, *38*(8), 653-663. https://doi.org/10.1071/WR10211.

Vamberger, M., Anunciação, P., Hofmeyr, M., et al (2019a). Mind the gap—Is the distribution range of *Pelomedusa galeata* really disjunct in western South Africa. *Amphibian & Reptile Conservation*, *13*, 57–60. Retrived from: http://amphibian-reptile-conservation.org/pdfs/Volume/Vol_13_no_2/ARC_13_2_%5bSpecial_Section%5d_57-60_e185.pdf.

Vamberger, M., Hofmeyr, M.D., Cook, C.A., et al (2019b). Phylogeography of the East African Serrated Hinged Terrapin *Pelusios sinuatus* (Smith, 1838) and resurrection of *Sternothaerus bottegi* Boulenger. *1895 As A Subspecies P Sinuatus. Amphibian Reptile Conservation*, *13*, 42–56. Retrived from: http://www.amphibian-reptile-conservation.org/pdfs/Volume/Vol_13_no_2/ARC_13_2_[Special_Section]_42-56_e184.pdf.

Vamberger, M, Hofmeyr, MD, Ihlow, F, et al. (2018). In quest of contact: phylogeography of helmeted terrapins (*Pelomedusa galeata, P. subrufa* sensu stricto). *PeerJ*, *6*, e4901. https://doi.org/10.7717/peerj.4901.

Watson, KP, & Granger, RA (1998). Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). *J Exp Biol*, *201(17)*, 2497–505. https://doi.org/10.1242/jeb.201.17.2497.

Whittington, M., Malan, G., & Panagos, M. D. (2013). Trends in waterbird diversity at Banzi, Shokwe and Nyamithi pans, Ndumo Game Reserve, South Africa. *Ostrich*, *84*(1), 47-61. https://doi.org/10.2989/00306525.2013.775188.