



## Thermal profiles associated with nest site selection of Nile crocodiles (*Crocodylus niloticus*) on a commercial crocodile farm

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### ABSTRACT

Understanding crocodile nest site selection is important in the context of climate change and related habitat alterations. This study assessed a current nesting environment on a crocodile farm in South Africa, examining associations between various nest site selection parameters, with a particular emphasis on the role of temperature. It was hypothesized that thermal profiles of nests and factors affecting nest temperatures (orientation, shading, grassy cover) would directly impact nest site selections, nests closer to waterbodies would be preferred, dominant females would dictate nesting area use, and human presence would not impact nesting behaviours as farmed crocodiles are accustomed to this. Nile crocodiles in this study produced nests of similar depth to wild Nile crocodiles, and subsurface temperatures varied with nesting layouts (section, orientation, shading), climate factors, and grass growth. Although a complex interaction of factors affected nest site selections, mean subsurface nest temperatures tended to fit into the narrow range of 25–26 °C, highlighting a measure of stability within the nesting environment. Daily temperatures and temperature ranges did however vary significantly between crocodile-selected nesting depths. Behaviour played an important role in the nest site selections, highlighting how nesting sites must be more than just thermally viable in farmed settings. Grassy growth over nesting sites reduced the surface and subsurface temperatures of those nests. Although this did not affect nesting site occupancy, crocodiles selected against depositing eggs in these sites. Nests closer to waterbodies and tourist walkway were occupied more frequently; however, successful nesting occurred further from the walkway. The size (snout-hindlimb length) of crocodiles within nesting sites did not correlate to preferred nesting sections within the pen. Further research is needed to determine if thermally optimal nesting conditions might be complicated by climate change related nesting environment alterations on commercial farms.

### 1. Introduction

Direct and indirect effects of climate change on nest-building animals have been studied (McGaugh and Jansen, 2011; Refsnider, 2012; Telemeco et al., 2013; Mainwaring et al., 2017), and quantification of reptilian/crocodilian thermal regimes regarding nesting strategies is important for the future of these populations (Morjan, 2003; Murray et al., 2016; Sullivan et al., 2022; Fukuda et al., 2022). Studying farmed/captive crocodile nest site selections and nesting conditions enables exploration of controlled criteria for nest site selection and thermal

preferences, facilitating hypothesis testing and novel methodological approach refinements. Notably, the “determining features” of, and factors influencing, nest site utilization/preferences for farmed crocodiles will vary from those of wild populations in natural environments.

Nesting activities have been documented for a variety of reptilian species (Swanepoel et al., 2000; Telemeco et al., 2013; Murray et al., 2020), including the Nile crocodile (*Crocodylus niloticus*). Nest site selection and nesting success are influenced by temperature, soil composition, water proximity, height above water, vegetation cover, human disturbance, and historical nest site use (Pooley and Gans, 1976; Kofron,

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1989; Hartley, 1990; Swanepoel et al., 2000; Botha, 2005; Maciejewski, 2006; Grigg, 2015). Crocodylian nest site selections vary with species, location, female experience, and nearby competing nesting females (Murray et al., 2020). Female egg-laying behaviours can depend on environmental cues like temperature and day length, with crocodylians nesting seasonally (Kofron, 1989; Swanepoel et al., 2000; Refsnider, 2012; Murray et al., 2020). Successful breeding, nesting, incubation, and hatching for captive populations are influenced by environmental temperatures, population genetic variability, general health of the breeding population, and husbandry practices (Bothma and Van Rooyen, 2005; Maciejewski, 2006; Bassetti et al., 2014; López-Luna et al., 2015; Manolis and Webb, 2016). Temperature-dependent sex determination (TSD) is well documented in crocodylians, where incubation temperatures determine the sex of the hatchlings (Deeming, 2004; Bothma and Van Rooyen, 2005; López-Luna et al., 2015). Consistently high (>34 °C) and low (<31 °C) temperatures yield predominantly female hatchlings whilst intermediate temperatures yield predominantly males (Hutton, 1987; Deeming, 2004; Bothma and Van Rooyen, 2005). Commercially farmed crocodile eggs are incubated artificially under strict temperature (29–33 °C) and humidity (90–99 % relative humidity) regimes to maximize hatching success (Bolton, 1989; Bothma and Van Rooyen, 2005; Tosun, 2013; Manolis and Webb, 2016). In wild populations, nest site selections are important in the context of reproductive success. Nest temperatures influence hatching success, sex ratios (and therefore population longevity), and hatchling size and survivability (Deeming, 2004; Charruau, 2012; López-Luna et al., 2015). Other factors affecting reproductive successes for wild crocodile nests include flooding, nest site cover variations, and predation risks (Leslie and Spotila, 2001; Combrink et al., 2016; Calverley and Downs, 2017; López-Luna et al., 2020).

Concerns regarding temperature dependent sex determination in wild reptilian populations being diverted by climate change have been considered; skewed potential sex ratios and increased egg mortalities may jeopardize the stability of such populations (Maciejewski, 2006; Refsnider, 2012; Telemeco et al., 2013; Hill et al., 2015). Incubation temperatures may also influence hatchling fertility and the pre-determination of preferred temperature ranges later in life (Lang, 1987; Tosun, 2013; Manolis and Webb, 2016; Murray et al., 2020). Clutch size (metabolic heat), solar radiation exposure of nesting sites, rainfall, nest depth, shading, and diel cycle can significantly affect temperatures within nests (Hutton, 1987; Lang et al., 1989; Swanepoel et al., 2000; Botha, 2005; Charruau, 2012; Somaweera and Shine, 2013; López-Luna et al., 2015; Murray et al., 2016; López-Luna et al., 2020). Female crocodiles lay their eggs at depths providing relatively stable temperatures and adequate moisture for embryo development and survival (Bolton, 1989; Bothma and Van Rooyen, 2005; Grigg, 2015; Mainwaring et al., 2017; López-Luna et al., 2020). Wild female crocodiles exercise circuitous visitations to determine nest-site suitability, defend nesting sites from predation, and to minimize thermal exposure or keep the area over the nest dry when it rains by laying directly over nest sites (Kofron, 1989; Messel and Vorlicek, 1989; Van Weerd, 2010; Combrink et al., 2016).

Nest microclimates, in and around nesting sites, have been investigated for several crocodylian species (Luts and Dunbar-Cooper, 1984; Galván, 2006; Charruau, 2012; Somaweera and Shine, 2013; López-Luna et al., 2015; Murray et al., 2016; López-Luna et al., 2020; Bock et al., 2020; Amoah et al., 2021; Lara et al., 2021) including the Nile crocodile (Hutton, 1987; Leslie and Spotila, 2001). Reported mean incubation temperatures (eggs or modelled eggs present) for hole and mound nests ranged between approximately 29–35 °C and 27–35 °C, respectively. These studies all assessed wild crocodylian nesting sites but varied in region, species, nesting method, thermal monitoring equipment and recording frequencies, logger positioning within nests, and the phase of incubation that was monitored. Hutton (1987) found mean temperatures of wild Nile crocodile nests in Lake Ngezi, Zimbabwe were consistently lower than 31 °C, but warmer than mean maximum soil

temperatures (24.5 °C). The shallowest eggs experienced higher mean temperatures and daily temperature fluctuations of up to 10 °C, with occasional maximums of 35 °C. Leslie and Spotila (2001) did not place temperature loggers among eggs as the study focussed on the effect that an alien plant species (*Chromolaena odorata*) was having on the selection of nesting sites at Lake St Lucia, KwaZulu-Natal. Due to shading effects, this plant caused average soil temperatures to drop by 5–6 °C, with many female crocodiles abandoning digs when encountering the plants. Nesting sites in farmed crocodylian populations are more controlled and closely spaced than in the wild, with flat topography, sandy nest substrate, and more homogeneous site conditions. Farmed crocodiles endure frequent exposure to human disturbances, and shade cover over nesting sites differs between farms (Bothma and Van Rooyen, 2005; Brien et al., 2007). Environmental shifts resulting from climate change will not only affect nest microclimates, but maternal nesting behaviours as well. This could include the timing of nesting, the choice of nesting sites, and the architecture of the nests themselves (Bock et al., 2020). Farmed crocodiles will not have the same opportunities to alter their nesting sites, strategies, or architectures like their wild counterparts. There is very little information available for farmed crocodile nesting experiences. Incubation temperatures and therefore skewed sex ratios might be under control (artificial incubation), but farms should monitor their breeding female nesting behaviours, strategies (nest dimensions and nest site selections), and successes.

Thermal and spatial characteristics of “preferred” nesting sites and nest occupancy on commercial crocodile farms have yet to be assessed to our knowledge. The present study aimed to assess the current nesting environment on a crocodile farm in South Africa, examining the associations between various nest site selection parameters, with a particular emphasis on the role of temperature. It was hypothesized that the thermal profiles of nesting sites and the factors affecting nest temperatures (depth, orientation, shading, and grassy cover) would directly impact nest site selections, larger and presumably more dominant females would dictate nesting area use, nests closer to water bodies would be more frequently utilized, and that human presence would not impact nesting behaviours as these crocodiles were habituated. The following parameters were studied using drones (one with thermal capabilities) and a selection of iButtons: surface and subsurface nest thermal profiles, pen substrate utilization, nest site occupancy versus active nesting, nesting female size and distribution over nesting sites, nest location and orientation selections, shading and grassy cover effects over nests, distances from the water bodies, and potential human disruptions.

## 2. Materials and methods

### 2.1. Study site

A single large breeder pen (5020 m<sup>2</sup>), on a crocodile farm in South Africa, was assessed over a single nesting season (October–December 2022). The open-aired enclosure contained three water bodies with gradient depths (maximum 2 m), each surrounded by concrete basking areas. Several large areas of grass and sand were interspersed between the water bodies. Nesting areas, cordoned off with short brick walls for nest separation, were dispersed throughout the pen, and these were the only areas with suitable nesting sand. Henceforth, pen substrates will be referred to as “water” for water bodies, “concrete” for the surrounding basking areas, “grass/sand” for interspersed grassy areas, and “nests” for the partitioned nesting sites.

There were 126 partitioned nesting sites available in the breeder enclosure, each was numbered and assigned to six “sections” by location within the pen, henceforth referred to as sections A–F (Supplementary Fig. A1). Within sections, the nests varied in orientation, i.e. “the compass direction that each nest-opening faced”. Four orientations were defined: Southeast (SE), Northeast (NE), Southwest (SW), and Northwest (NW) facing (Supplementary Table C1). A pedestrian tourist walkway extended partially into the pen. This walkway was situated at

ground level, flanked by brick walls and safety fencing, and included a sheet-metal roof. Shading (time of day dependent) was provided by the tall brick perimeter walls of the pen, trees external to and within the pen, shade netting, and the walkway roof.

Two hundred and thirty-three breeder Nile crocodiles, ranging in snout-hindlimb lengths (SHL) from 1.2 to 2.4 m, were counted within the pen. SHL is a measure like snout-vent length, adapted for drone-based length measurements, and is measured from “the tip of the snout to the circumcircle scute layer immediately posterior to the back legs” (Myburgh, 2021; Viljoen et al., 2023a). If this feature was not identifiable for a crocodile, this morphometric was omitted for that animal. Personnel assigned to the pen remained consistent throughout the nesting season. Climate data were obtained from South African Weather Services (SAWS) and Weather Underground (<https://www.wunderground.com/>) weather stations nearest the farm, 11.29 km and 8.15 km away, respectively. Hourly air temperatures (°C), relative humidity (% RH), rainfall (mm), wind speed (m/s), and solar radiation ( $W/m^2$ ) data were incorporated into this study. Solar radiation data specifically was from the Weather Underground station as this variable was not recorded by the SAWS station. These environmental descriptors were included as potential influencers of soil and nest temperatures (Hutton, 1987; Leslie and Spotila, 2001; Bock et al., 2020; Charruau, 2012; Lehnert, 2014; Zhang et al., 2016), and as known influencers of farmed Nile crocodile behaviour (Viljoen et al., 2023b). As this study included soil temperature recordings at relatively shallow depths (maximum 40 cm below ground level), these variables were selected for proposed direct heat input effects (temperature and radiation) and the effects on heat exchange, moisture content, and thermal conductivity (wind speed, humidity, and rainfall) of the soil.

## 2.2. Thermal profiles within nests

Subsurface thermal properties of a selection of nests were assessed using Liquid Armour (<https://liquidarmour.co.za/>) coated iButtons (DS1921G-F50 Thermocron), secured in 3D printed holders (Supplementary Fig. A2a), which recorded hourly temperatures for the full study period. Liquid Armour was used as a waterproofing agent and is like PlastiDip, the effects of which on iButton temperature recordings has been previously assessed (Roznik and Alford, 2012). This former study found relatively small temperature variations between encapsulated and unencapsulated iButtons, ranging between 0 °C and 1.3 °C when iButtons were placed in direct sunlight at the warmest time of the day. IButton holders were printed with a Creality Ender-3 V2 3D printer, using PLA + plastic; the holder design was publicly accessible on Thingiverse (design reference number: 2895204). Nest depths were evaluated early in the nesting season to identify appropriate depths for this assessment (Supplementary Appendix B); notably, the breeder pen utilized for this study contained exclusively fine-sanded nests. Twenty-four iButtons were placed in six partitioned nesting sites (four per site) which differed in location and orientation. IButtons were tied onto brightly coloured (spray painted) wooden dowels and inserted vertically into selected nests so that depths 10, 20, 30, and 40 cm below ground surface level were recorded (Supplementary Fig. A2b). The dowels ensured the iButtons remained in place and improved visibility should the dowel be exposed due to crocodiles digging in the vicinity. Nests were checked daily; no dowels were dug up during the study. Nests containing these evenly spaced iButtons will be referred to as “dowel” nests.

Nine iButtons measured single-depth temperatures in randomly selected, confirmed nests (i.e., eggs were deposited in these nest sites), as they were being harvested. These iButtons were tied onto a brightly coloured rope (for visibility during extraction) and tagged using key tags (Supplementary Fig. A2c). Each iButton was inserted at the depth of the deepest egg, after which the nest was covered. Nests with single loggers will be referred to as “single” harvested nests. The farm harvested eggs from nests daily (South African Bureau of Standards, 2009), therefore

eggs were not left in the nesting sites long enough for loggers to be placed among them. Instead, this study evaluated the nesting environment, identifying potential factors influencing nest site selection and nest depth.

## 2.3. Surface and crocodile temperature variations

On December 1, 2022, hourly thermal mapping flights (from 07:00–15:00) were conducted using a Mavic 2 Enterprise Dual drone as per Viljoen et al. (2023b). The imagery was processed in OpenDroneMap (ODM, version 1.9.3 build 30) and imported into QGIS (version 3.16-Hannover) (QGIS Development Team, 2021) following the methods of Myburgh et al. (2024). Thermal data for the pen (all substrates), nesting sites (surface temperatures, area shading ratio, grass growth), and crocodiles (“back” and “positional” temperatures) were determined (Viljoen et al., 2023b) using point layers and zonal statistic extractions from polygon layers (“join attributes” function). SHLs were recorded with line-string layers (Viljoen et al., 2023a). Polygon layers outlined distinct surface substrates (water, concrete, grass/sand, nests) and distinguished nesting sites by number. Hourly proportional shading over each nesting site was calculated using zonal statistic layers and classified into five categories, each representing bins of 20 percent (0–19 %, 20–39 %, 40–59 %, 60–79 %, 80–100 %). Nests were categorized based on the presence or absence of grass; proportional coverage was avoided due to heterogeneous grass dispersion across nesting sites.

## 2.4. Crocodile pen and nest utilization

A DJI Mini 2 SE drone was flown once per week, on a randomly selected day of the week, in the morning (06:00–07:00) and afternoon (15:00–17:00) for seven weeks during the nesting season. A midday flight (12:00–12:30) was included on three occasions. These observation periods were dependent on the drone operator’s availability, who also worked on the farm. Identical flight paths and parameters were used as for the Mavic 2 Enterprise Dual drone flights and data were processed as per Myburgh et al. (2021). Behavioural data (pen area utilization, nest occupancy, nest utilization, nesting section/orientation preferences) were recorded with drone imagery and farm nest records for the nesting season. “Nest occupancy” refers to the crocodiles occupying a nesting site during the observation periods, whereas nest “utilization” refers to the committed use (i.e., eggs deposited) of a nesting site. The total number of nesting sites occupied and utilized per section were normalized by the total nest count within that section, controlling for potential biases favouring sections with a greater number of nesting sites. Distances from each nests’ entrance to the closest water body and tourist walkway were extracted from drone imagery using line-string layers (Supplementary Table C1). Crocodile positions and SHLs were recorded for each time slot using the layer types described previously.

## 3. Data analysis

Data were captured in Excel and analysed in R (2022.12.0 Build 353) and IBM SPSS Statistics (version 28). The following R packages were utilized: readr, rlang, ggplot2, ggpmisc, dplyr, tidyr, lubridate, rcompanion, car, chisq.posthoc.test, lme4, lmerTest, multcomp, vcd, betareg, stats (R Core Team, 2022). Summary statistics allowed visualization of the data distribution, identification of potential outliers, and assessment of fundamental characteristics of the data. The data was tested for normal distribution. Chi square analyses were done to compare observed proportional nest utilization (drone data) and confirmed egg depositions (farm records) across nesting sections and orientations, whilst controlling for the variable number of nests in each of these categories. Univariate general linear models (GLM), with subsurface soil temperature as the dependent variable, were used to elucidate the effects of climate variables (ambient temperature, relative humidity, windspeed, solar radiation, rainfall), depth, nest section and orientation, nest type

(whether the temperature loggers were in a dowel- or single-nest), grassy growth over nesting sites, and time of the day (AM or PM). Nest type and depth were fixed factors in the initial model, which focussed on the effects of climate variables on subsurface nest temperatures. To avoid redundancies, confounded variables (e.g., section and orientation) were not assessed in the same model. Single and dowel temperatures were also assessed separately to ensure there were no confounding outcomes resulting from those depths that were researcher versus crocodile selected. Mixed model analyses were incorporated for this purpose and a Residual Maximum Likelihood Model (REML) accommodated for the unbalanced nature of the data. Pearson product moment correlations were used to determine relationships between variables, only after these variables were determined as having had a significant effect on the dependent variable. Analyses of Variance (ANOVA) and a GLM were used to assess the factors influencing surface level soil temperatures, crocodile back temperatures and shading over nesting sites. Post hocs (Bonferroni) were conducted to determine specific pairwise group differences. All data were analysed for the determination of significant differences at  $P < 0.05$ , highly significant differences were noted where  $P < 0.001$ .

## 4. Results

### 4.1. Study site

During the study period, air temperature ranged from 12.8 to 36.8 °C ( $\bar{x} = 22.8$  °C, SE = 0.1 °C), relative humidity from 10 to 97 % RH ( $\bar{x} = 63.1$  % RH, SE = 0.5 % RH), rainfall from 0 to 17 mm ( $\bar{x} = 0.1$  mm, SE = 0.0 mm), wind speed from 0 to 6.4 m/s ( $\bar{x} = 1.1$  m/s, SE = 0.0 m/s), and solar radiation from 0 to 795.7 W/m<sup>2</sup> ( $\bar{x} = 160.5$  W/m<sup>2</sup>, SE = 5.1 W/m<sup>2</sup>) (Supplementary Fig. A3).

### 4.2. Thermal profiles within nests

Of the 33 iButtons deployed, one was not recovered from a dowel in section F and another in section C (19.5 cm depth) malfunctioned, the outputs were therefore not included in the analyses. Subsurface nest temperatures were significantly affected by nest orientation ( $P < 0.05$ ,  $F = 4.833$ ,  $df = 1$ ), section ( $P < 0.001$ ,  $F = 54.503$ ,  $df = 2$ ), depth ( $P < 0.001$ ,  $F = 92.184$ ,  $df = 10$ ), grassy growth ( $P < 0.001$ ,  $F = 259.637$ ,  $df = 1$ ), and hour of the day ( $P < 0.001$ ,  $F = 254.790$ ,  $df = 23$ ). A significant interaction effect between orientation and section was noted ( $P < 0.001$ ,  $F = 40.975$ ,  $df = 1$ ), indicating the impact of these variables depend on one another to an extent, therefore the main effects should be interpreted with caution. Nest temperatures were significantly influenced by air temperature ( $P < 0.001$ ,  $F = 955.530$ ,  $df = 1$ ), relative humidity ( $P < 0.001$ ,  $F = 5123.332$ ,  $df = 1$ ), solar radiation ( $P < 0.001$ ,  $F = 8553.210$ ,  $df = 1$ ), wind speed ( $P < 0.001$ ,  $F = 69.837$ ,  $df = 1$ ), and rainfall ( $P < 0.001$ ,  $F = 640.303$ ,  $df = 1$ ). Nest temperatures were positively correlated with air temperatures ( $r = 0.43$ ,  $P < 0.001$ ), windspeed ( $r = 0.12$ ,  $P < 0.001$ ), and radiation ( $r = 0.05$ ,  $P < 0.001$ ); negatively correlated with relative humidity ( $r = -0.52$ ,  $P < 0.001$ ); and not significantly correlated to rainfall ( $P > 0.05$ ). In dowel-nests, the strength of correlations between nest temperatures and all climate variables decreased with increasing depth, remaining significant at all depths for all variables except rainfall. At 10 cm below ground level, nest temperatures were correlated with rainfall ( $r = -0.06$ ,  $P < 0.001$ ); this did not hold true for depths  $\geq 20$  cm ( $P > 0.05$ ). Single harvested nest temperatures were not correlated to rainfall ( $P > 0.05$ ). Nest temperatures were positively correlated to hour of the day ( $r = 0.27$ ,  $P < 0.001$ ).

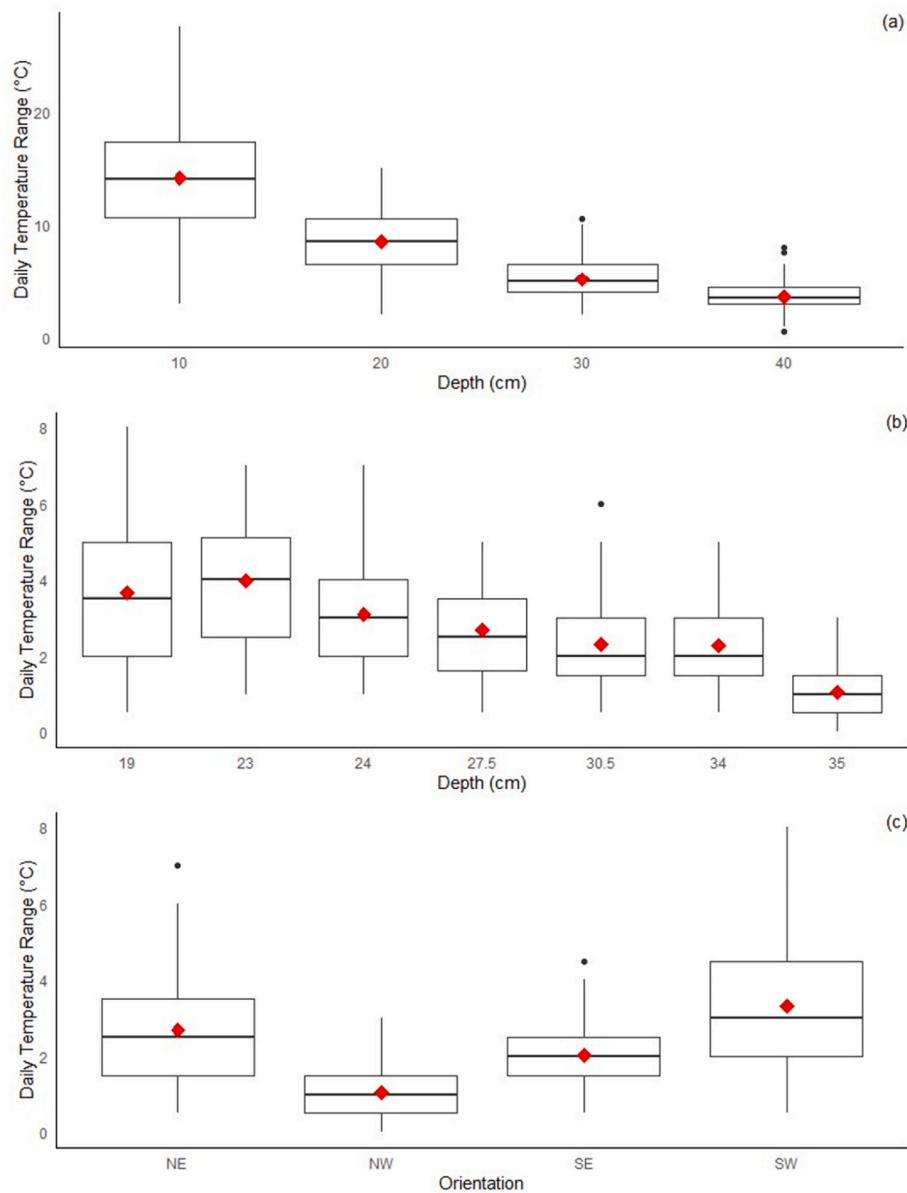
Based on descriptive trends (Supplementary Table C2), as depths within dowel nests increased from 10 to 40 cm, minimum temperatures increased, maximums and ranges decreased, and means remained comparable. Section A dowel-nest temperatures ranged from 15.5 to 49.5 °C and those in section F from 15 to 46.5 °C. Temperatures at the varying depths differed highly significantly ( $P < 0.001$ ,  $F = 78.97$ ,  $df =$

3) from one another, except between 20 and 30 cm depths where they differed significantly ( $P < 0.05$ ) (Supplementary Fig. A4a). Minimum temperatures recorded in single nests ranged from 19.5 to 22 °C, maximums from 30.5 to 32.5 °C, and means from 24.6 to 26.2 °C (Supplementary Table C3). Single-iButton temperatures varied significantly from one another ( $P < 0.001$ ,  $F = 60.89$ ,  $df = 6$ ), exceptions to this finding ( $P > 0.05$ ) were noted between the depths of 35 cm to 23, 24, 27.5 and 34 cm, 24 cm to 23 and 27.5 cm, and 23 cm to 34 cm (Supplementary Fig. A4b).

Dowel nest temperatures varied significantly with section ( $P < 0.001$ , SE = 0.030,  $z = -56.777$ ), and therefore orientation there was as only one orientation within each section for dowel loggers. Section F nests (NE facing) had higher mean temperatures than section A nests (SE facing). Orientation and section effects on nest temperatures were assessed separately for single iButtons, as these represented crocodile-selected sections and orientations. NE facing nests had the highest mean temperatures ( $\bar{x} = 25.86$  °C), followed by NW ( $\bar{x} = 25.52$  °C), SW ( $\bar{x} = 25.46$  °C), and SE facing nests ( $\bar{x} = 24.55$  °C) (Supplementary Fig. A5). Among single iButton loggers, nest temperatures varied significantly with nest orientation ( $P < 0.001$ ,  $F = 171.8$ ,  $df = 3$ ), between all orientations ( $P < 0.001$ ) except SW and NW facing nests ( $P > 0.05$ ). Single-iButton nest depths per orientation were tentatively assessed, dowel-iButton nests were excluded as these depths were not selected by the crocodiles. NW facing nests had the highest mean nest depths ( $\bar{x} = 35$  cm) followed by SE ( $\bar{x} = 34$  cm), NE ( $\bar{x} = 27.3$  cm), and SW facing nests ( $\bar{x} = 25.6$  cm). Nest depths varied significantly with orientation ( $P < 0.001$ ,  $F = 3508$ ,  $df = 3$ ), where all orientations varied from one another ( $P < 0.001$ ). Mean subsurface temperatures per nesting sections A–D and F were 24.55 °C, 25.03 °C, 25.52 °C, 25.85 °C, and 25.79 °C, respectively. Nest temperatures varied significantly with nest section ( $P < 0.001$ ,  $F = 160$ ,  $df = 4$ ), between all sections ( $P < 0.001$ ) except D and F ( $P > 0.05$ ).

Daily nest temperature ranges varied significantly with depth ( $P < 0.001$ ,  $F = 72.852$ ,  $df = 10$ ) and orientation ( $P < 0.001$ ,  $F = 37.062$ ,  $df = 3$ ). Specifically, as depths increased the temperature ranges decreased (Fig. 1a). When assessing dowel-fitted nests exclusively, SE (section A) and NE (section F) facing nests exhibited mean daily temperature ranges of 7.49 °C and 8.21 °C, respectively. Post hoc comparisons revealed significant differences between daily temperature range means between all dowel depth categories ( $P < 0.001$ ). When assessing single iButton-fitted nests exclusively, mean daily nest temperature ranges varied from 1.05 to 3.99 °C (Fig. 1b). Mean daily nest temperature ranges differed significantly between the depth of 19 cm and those  $\geq 27.5$  cm ( $P < 0.001$ ). Mean ranges recorded at depths of 23 and 24 cm did not differ from those recorded at 19 cm below ground level ( $P > 0.05$ ). Mean ranges at 23 cm deep varied significantly from those  $\geq 24$  cm deep ( $P < 0.001$ ), and those at 24 cm deep varied from depths  $\geq 30.5$  cm ( $P < 0.001$ ). Mean ranges differed significantly between 35 cm below ground surface level and all other depths ( $P < 0.001$ ). Mean daily nest temperature ranges varied significantly between all orientations when assessing the single iButton-fitted nests ( $P < 0.001$ ). Ranked by their daily temperature ranges, SW facing nests had the highest mean range ( $\bar{x} = 3.328$  °C), followed by NE ( $\bar{x} = 2.701$  °C), SE ( $\bar{x} = 2.020$  °C), and NW ( $\bar{x} = 1.052$  °C) facing nests (Fig. 1c).

No dowel-nests had grassy growth, whereas four single-nests with depths: 19, 30.5, 34, and 35 cm (iButtons 32, 28, 31, and 33, respectively) did. Subsurface temperatures of grassy nests were significantly lower than those of nests without grass ( $P < 0.001$ , SE = 0.037,  $z = 10.697$ ). The 19, 34, and 35 cm depth nest temperatures were significantly affected by grassy cover ( $P < 0.001$ ,  $t = 6.130$ ,  $df = 1380.4$ ;  $P < 0.001$ ,  $t = 14.725$ ,  $df = 1198.6$ ;  $P < 0.001$ ,  $t = 15.932$ ,  $df = 971.0$ , respectively). These nests were in unique sections and orientations, precluding further comparisons.



**Fig. 1.** Daily sand temperature ranges of the dowel iButtons arranged by depth (a), single iButtons arranged by depth (b), and single iButtons arranged by orientation (c). Each boxplot displays the median (centre line), interquartile range (box edges), and 1.5 \* IQR (whiskers). Points beyond whiskers represent outliers and red rhombuses represent means.

#### 4.3. Surface and crocodile temperature variations

On December 1, 2022 (for descriptive statistics see [Supplementary Table C4](#)), crocodile back temperatures varied with selected pen substrates ( $P < 0.001$ ,  $F = 112.99$ ,  $df = 3$ ), where crocodiles in water had significantly lower back temperatures than those on other substrates (all  $P < 0.001$ ) and no other substrates differed significantly regarding this measure ( $P > 0.05$ ). Back temperatures of crocodiles occupying nesting areas did not vary with nest orientation or section ( $P > 0.05$ ).

Nest surface temperatures varied significantly with shading ( $P < 0.001$ ,  $F = 140.048$ ,  $df = 1$ ), section ( $P < 0.001$ ,  $F = 22.468$ ,  $df = 4$ ), grassy cover ( $P < 0.001$ ,  $F = 301.345$ ,  $df = 1$ ), and hour of the day ( $P < 0.001$ ,  $F = 288.891$ ,  $df = 8$ ). As proportional shading over nesting sites increased, nest surface temperatures decreased. The mean nest surface temperatures for increasing shading bins were: 44.53 °C (0–19 % shading), 37.71 °C (20–39 % shading), 28.10 °C (40–59 % shading), 22.98 °C (60–79 % shading), and 21.34 °C (80–100 % shading). Nest surface temperatures between all shading bins differed significantly ( $P$

$< 0.05$ ) from one another, except the fourth and fifth (representing 60–100 % shading). Sections D and F's nest surface temperatures varied significantly from those of all other nesting sections ( $P < 0.001$ ), and from one another ( $P < 0.001$ ) ([Fig. 2a](#)). The remaining nesting sections did not vary significantly ( $P > 0.05$ ) from one another regarding surface temperatures ([Supplementary Table C5](#)). Nests with grass growth ( $\bar{x} = 36.24$  °C) had significantly lower surface temperatures than those without ( $\bar{x} = 46.10$  °C) ([Fig. 2b](#)). Mean nest surface temperatures varied significantly ( $P \leq 0.05$ ) between all hours of the day except 09:00 and 14:00, 10:00 and 15:00, 12:00 and 13:00, and 14:00 and 15:00. Nest surface temperatures did not significantly vary with nest orientation ( $P > 0.05$ ).

Shading over nesting sites varied significantly with section ( $P < 0.001$ ,  $F = 9.89$ ,  $df = 4$ ), orientation ( $P < 0.001$ ,  $F = 26.52$ ,  $df = 2$ ), and hour of the day ( $P < 0.001$ ,  $F = 288.89$ ,  $df = 8$ ). Mean shading percentages for nest sections A–F were 11.67 %, 22.03 %, 21.13 %, 16.87 %, 16.77 %, and 22.08 %, respectively. Section A varied significantly from sections B ( $P < 0.001$ ), C ( $P < 0.05$ ), and F ( $P < 0.001$ ) regarding

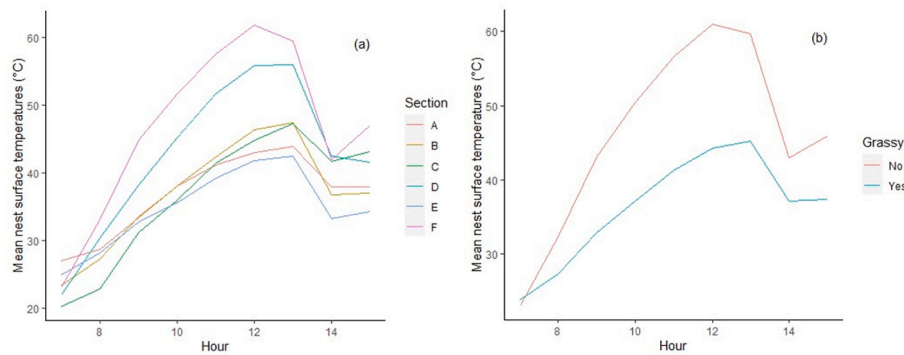


Fig. 2. Mean hourly nest surface temperatures by (a) nesting section and (b) grass-cover status of the nesting site.

shading, as did section F from section D ( $P < 0.05$ ) (Supplementary Fig. A7a). Mean shading percentages for the nest orientations NE, NW, SE, and SW were 20.02 %, 21.13 %, 11.20 %, and 21.02 %, respectively. Shade cover of SE facing nests was significantly lower than all other orientations ( $P < 0.001$ ), other orientations did not vary ( $P > 0.05$ ) (Supplementary Fig. A7b).

#### 4.4. Crocodile pen and nest utilization

Proportional substrate occupancy varied significantly between all time-of-day categories ( $P < 0.001$ ,  $\chi^2 = 561.80$ ,  $df = 6$ ) (Supplementary Fig. A8). Occupancy of nests was greatest in the afternoon, followed by morning, and finally midday. Water occupancy showed the opposite pattern, where 73 % of crocodiles within view during midday flights occupied waterbodies. The grass/sand substrate was least frequently occupied at all times of the day. Nest occupancy varied significantly with air temperatures ( $P < 0.001$ ,  $z = 5.001$ ,  $\beta = -0.055$ ,  $SE = 0.002$ ) and solar radiation ( $P < 0.001$ ,  $z = -11.722$ ,  $\beta = -0.007$ ,  $SE = 0.001$ ), but was unaffected by grassy cover ( $P > 0.05$ ). Nest occupancy varied significantly with the distance of nests from the closest water bodies ( $P < 0.05$ ,  $t = -2.091$ ,  $\beta = -0.129$ ,  $df = 89.18$ ) and walkway ( $P < 0.05$ ,  $t = -3.259$ ,  $\beta = -0.127$ ,  $df = 69.39$ ). Specifically, nests closer to water and the walkway were occupied more often. Nesting section confirmations (i.e., eggs recovered) were significantly affected by distance from the walkway ( $P < 0.05$ ,  $t = 3.616$ ,  $\beta = 0.089$ ,  $df = 17.19$ ), but not distance from the closest water body ( $P > 0.05$ ). Specifically, confirmed nests were more frequent at nesting sites further from the walkway.

An association between nest occupancy in the drone imagery and confirmed nests excavated across different nesting sections was found ( $P < 0.001$ ,  $\chi^2 = 5878.8$ ,  $df = 1$ ). However, limited overlap between the drone and farm datasets precluded a statistical confirmation of this association per nesting section. Both nest occupancy ( $P < 0.001$ ,  $\chi^2 = 99.886$ ,  $df = 5$ ) and confirmed nesting ( $P < 0.001$ ,  $\chi^2 = 49.195$ ,  $df = 5$ ) showed significant variation across different sections when assessed

separately (Fig. 3).

Nesting section C was most frequently occupied (34 %), and section F was most frequently nested in (38 %). Nesting section E was least frequently occupied (11 %) and nested in (0 % - rounded). Sections A, B, D, and F had intermediate occupancy with proportions of 13 %, 14 %, 13 %, and 15 %, respectively. Sections A–D had nest utilization proportions of 11 %, 17 %, 17 %, and 16 %, respectively. Nesting sections were preferentially occupied and utilized in the following orders:  $C > F > B > A & D > E$  and  $F > B & C > D > A > E$ , respectively. Both nest occupancy ( $P < 0.001$ ,  $\chi^2 = 113.3$ ,  $df = 3$ ) and nest utilization ( $P < 0.05$ ,  $\chi^2 = 9.784$ ,  $df = 3$ ) showed significant variation across different orientations. Nests facing NW were most frequently occupied (46 %), followed by NE (23 %), and SE and SW facing nests (both 16 %). Orientation NE was nested in most frequently (36 %), followed by NW and SW (both 23 %), and SE (18 %). As the nesting season progressed, grass began growing into some nesting sites, these nests produced significantly less (i.e., eggs deposited) than those without ( $P < 0.001$ ,  $\chi^2 = 28.571$ ,  $df = 1$ ).

Mean SHLs of crocodiles per substrate type, nesting section, and nesting orientation were ordered as follows: concrete > water > grass/sand > nests,  $C > B > D > F > A > E$ , and  $NW > NE > SW > SE$ , respectively (Supplementary Fig. A9). SHLs of crocodiles occupying the different substrates varied significantly ( $P < 0.001$ ,  $F = 63.84$ ,  $df = 3$ ). Specifically, crocodiles occupying nests were shorter than those occupying all other substrates ( $P < 0.001$ ). Crocodiles occupying concrete areas had longer SHLs compared to those occupying grass/sand areas ( $P < 0.001$ ). SHLs of crocodiles within nesting areas varied significantly with section ( $P < 0.001$ ,  $F = 14.970$ ,  $df = 5$ ) and orientation ( $P < 0.001$ ,  $F = 8.667$ ,  $df = 2$ ). Mean SHLs recorded in section C (and therefore orientation NW, as no other sections contained nests with this orientation) were significantly greater than those for all other sections ( $P < 0.001$ ), no other sections varied ( $P > 0.05$ ).

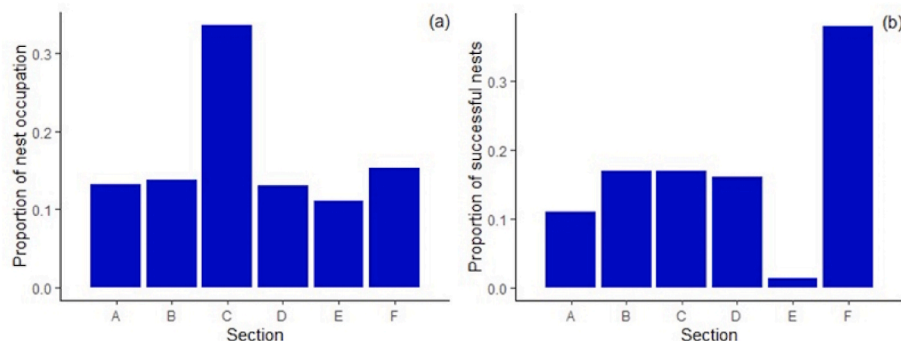


Fig. 3. The proportional nest site occupancy (a) and confirmed nesting successes (b) per nesting section.

## 5. Discussion

### 5.1. Thermal profiles within nests

Subsurface nest temperatures were influenced by climatic conditions, nest site location/orientation, nest depth, and grass cover. Thermal inertia slowed heating from ambient temperatures and radiation at deeper depths. As relative humidity increased, nest temperatures decreased. The strength of this correlation diminished as soil depths increased, supporting the established relationship between relative humidity and soil moisture content, and subsequently, soil thermal inertia. Although there was relatively little rainfall during the study, the effect on shallower nest temperatures was intuitive, the cooling effect lessened with increasing depths. Shading, depth, air temperature, rainfall, and solar radiation all influenced nest temperatures in the current study in a similar manner as clutch (with eggs or modelled-eggs present) temperatures from former studies have reported (Hutton, 1987; Charruau, 2012; Somaweera and Shine, 2013; Bock et al., 2020; López-Luna et al., 2020). This highlights the importance of climate and nest depths as primary factors affecting subsurface nest temperatures, even when eggs were not present for the current study.

Section F dowel iButtons recorded higher temperatures and greater daily temperature ranges than in section A. These sections differed in daily shade percentages (orientation based) and nest surface temperatures. Differential sunlight, wind, and shade exposure likely contributed to observed variations in nest surface temperatures between the sections (Somaweera and Shine, 2013; Bock et al., 2020; López-Luna et al., 2020; Lara et al., 2021). Single nest depths ranged from 19 to 35 cm, and although mean temperatures fell within 1.15 °C of one another and mean daily temperature ranges varied between 1.05 °C and 3.99 °C, recorded temperatures varied significantly. Nest depth selections varied between all orientations, whereas subsurface temperatures varied between all orientations except SW and NW facing nests. Nest surface temperatures did not vary with orientation, but shading proportions varied between SE facing nests and other orientations. These findings suggest female crocodiles may select nest depths, and therefore temperatures, based on orientation, independent of shading and nest surface temperatures; the rationale is unclear. Only sections D and F did not vary from one another regarding mean nest temperatures, these sections had the highest surface and subsurface nest temperatures. Grass growth over nests, likely enhancing the boundary layer effect, acted as a thermal buffer and reduced the direct impact of solar radiation on the sand below.

Mean temperatures at various depths (single and dowel nests) tended to fit into the narrow range of 25–26 °C, highlighting a measure of stability within the nesting environment. Shallower depths had greater daily temperature variations; Charruau (2012) and Hutton (1987) reported similar findings for American crocodile and Nile crocodile nests with eggs present. Similarly, western painted turtle (*Chrysemys picta bellii*) mean nest temperatures did not vary with nest depth, but the daily range in nest temperatures did vary (Refsnider, 2012). The effects of orientation (interpreted with caution) on daily temperature ranges were significant for all comparisons, suggesting orientation affected subsurface temperature ranges at various depths. A soil temperature study in China (1962–2011) found global warming effects occurred as deep as 3.2 m, with soil surface temperatures having increased 31 % more than air temperatures (Zhang et al., 2016). Although there are distinct climatic, geographical, and environmental differences between regions, the broader insights remain valuable. Nile crocodile nest depths fall well within 3.2 m of the ground surface, such temperature changes could pose challenges for incubation success, sex determination, and hatchling survival. A lizard (*Bassiana duperreyi*) changed nesting depths and timing in response to rising ambient temperatures, but the seasonal progression of soil temperatures had also shifted due to climate change. Unfortunately, their attempts at nest temperature remediation were unsuccessful and offspring sex ratios were affected (Telemeco et al.,

2009). Similarly, Bock et al. (2020) found that nest site selections were insufficient in buffering the current ambient environment and maintaining unbiased sex ratios for wild American alligators. Calverley and Downs (2017) studied Nile crocodile nesting behaviour and noted that wild crocodiles without suitable nesting sites are expected to nest elsewhere, often nesting in “clumps” and sometimes nesting many kilometres apart. In this study the crocodile population had tripled since the 1960s, but the nesting effort had not changed due to insufficient suitable nesting sites (Calverley and Downs, 2017). Farmed crocodiles have even less nest site selection flexibility (location, substrate) and, as can happen in wild Nile crocodile populations, might not nest every year if sufficient quality nesting sites are not available (Kofron, 1989; Calverley and Downs, 2017).

Although incubation and hatching are artificially managed on farms, nesting activities and behaviours of males during the nesting season and nesting females might be impacted by climate change. Habitat and nest quality alterations due to climate change necessitate adaptations by wild crocodile populations (Refsnider, 2012; Mainwaring et al., 2017; Fukuda et al., 2022). Farmed crocodiles do not have the same opportunity to adapt to changing environments by relocating, modifying nesting sites, or altering nesting materials. Consequently, there is concern regarding unmonitored changes in the immediate environment/habitats of commercially farmed crocodiles. From a nesting perspective this involves understanding and controlling for thermal and behavioural factors which influence nest site selections.

### 5.2. Surface and crocodile temperature variations

Crocodile back temperatures were affected by substrate selections, air temperature, relative humidity, and wind speeds. These findings, alongside the proportional hourly area/substrate use results, are consistent with ectothermy (Viljoen et al., 2023b). The crocodiles relinquished nesting behaviours during the warmest part of the day to seek out more thermally comfortable areas. This is analogous with Combrink et al. (2016) where wild female Nile crocodiles were rarely seen guarding nests diurnally unless there was nearby shade cover or during cooler/cloudy/rainy weather. Shade implementations nearby nesting sites on farms might benefit nesting females in terms of nest site guarding behaviours. Increasing radiation levels, temperatures, and relative humidity decreased the appeal of occupying nesting sites, indicating a thermal threshold for crocodile comfort in nest sites. Increased wind speeds may have altered the atmospheric boundary layer directly over the nests, making the nesting sites more thermally tolerable.

Nest section, shading, and grassy cover all impacted nest surface temperatures on December 1, 2022. Two nesting sections had significantly higher surface temperatures than the others. Section F had the highest nest surface temperatures, followed by section D. Interestingly, these sections also had higher mean subsurface temperature recordings (when referring to the single iButton data) than other sections.

### 5.3. Crocodile pen and nest utilization

Nest occupancy was linked to increasing air temperatures and radiation levels nearing midday, with crocodiles retreating to the water bodies or concrete. Nest defence and/or thermal protection would not have been prioritized if thermoregulatory requirements took precedence (Kofron, 1989; Swanepoel et al., 2000; Bourquin, 2008). Grass growth did not affect nest occupancy behaviours. More frequent occupation of nests closer to the walkway confirmed that crocodiles were not behaviourally impacted by human presence. However, confirmed nests were more frequent further from the walkway, countering the hypothesis that human presence would not impact nesting. This might be attributed to visitor activity/disturbance, a perceived predation risk, practise/decoy nesting (Lang et al., 1989; Kofron, 1989; Van Weerd, 2010), or other factors impacting nest-habitat quality. Wild Nile crocodiles avoid

nesting in areas with anthropogenic disturbances (Calverley and Downs, 2017); the crocodiles in the current study seemed to retain this awareness and avoided depositing eggs closer to the tourist walkway. Nests closer to water were occupied more frequently, likely due to easier access. Distance from water had no significant effect on successful nesting (i.e., egg deposition), contradicting that hypothesis. For wild Nile crocodiles, distance from water does not independently impact nest site selections, rather the relationship between this parameter and height above water (Swanepoel et al., 2000; Botha, 2005). These natural nests were dug on inclines, this is dissimilar to farmed crocodile experiences where nests are built with relatively flat topographies and height above water is set by the pen design.

Section F was frequented comparably with most other sections, was second highest in distance from the water and walkway and had the greatest confirmed nesting frequency. Section C had the highest occupancy frequency, but comparable confirmed nesting frequency with most other sections. Section E was interesting, it had a comparatively low distance from the walkway, the shortest average distance from water, and was frequented comparably with most other sections; however, it was least preferred for nesting. All sites within section E were grassy by the end of the nesting season; however, this section was least favoured for active nesting both before (one nest produced) and after (no nests produced) grassy growth. The negative impact of grassy growth in this study may be comparable to the study by Leslie and Spotila (2001), where wild Nile crocodiles dug in various locations but abandoned nest sites due to local plant-life. These wild crocodiles would still have been sighted in these areas even if eggs were not being deposited. However, it does not explain the minimal use of the section before the grass growth began. Another study noted that radiation did not have the expected influence over nest temperatures for American crocodiles due to the vegetation density and shaded canopy (Lara et al., 2021). Section A had the greatest mean distances from water and the walkway and was the second least preferred for nesting. It is noted that, although not as close as the tourist walkway, there was a building across from the external pen wall of that nesting section.

Shorter (SHL) individuals occupied nests; these were most likely nesting females. Larger females did not dominate preferred nesting sections within the pen, only section C had comparatively higher SHLs. It is possible that smaller females may not have approached nesting sites as readily, or that size is not an entirely reliable indicator of dominance. This study captured only a snapshot of nesting behaviours; further research would be needed to expand on these findings. Although climate data for the specific study site would have been preferred, the weather stations were relatively close to the farm and the enclosure was open to the air; nevertheless, this is acknowledged as a potential shortcoming of this study. Another limitation is common in studies where waterproofing of temperature loggers is required, the small temperature variations may be important for studies requiring precise temperature recordings.

## 6. Conclusions

Surface and subsurface nest temperatures were predominantly affected by the local climate factors, nest depths, time of day, and location (shading and grass growth over nest sites). While nest site location and orientation both affected subsurface nest temperatures statistically, there was an association between these two variables and so they were investigated separately, with a focus on section. Although farmed crocodiles' choices for nesting sites and sand types are more limited than in the wild, crocodiles in the current study selected nest depths comparable to those selected by wild Nile crocodiles. Whilst mean temperatures and daily temperature ranges within nests varied statistically, the real-world impact of these fluctuations requires further evaluation. Nest temperatures decreased with increasing sand depths, and temperatures recorded at deeper depths were less influenced by surface conditions. Grassy cover significantly affected nest surface and subsurface temperatures; these nests were selected against for egg laying

purposes.

Circuitous nest visitations likely contributed to the occupancy versus successful nesting findings, demonstrating the female crocodile's ability to recognize human presence as a potential predation risk to their clutches. Nesting section F was preferred for confirmed nests but had comparable occupancy rates with most other sections. This section had the highest mean nest surface temperatures, second highest subsurface temperatures, second highest mean proportional shading, and second highest distances from both the walkway and nearest water body. The findings herein showed a hierarchical preference for nesting sections within the pen, based upon a combination of influencing factors (thermal and behavioural). Larger, presumably more dominant, females did not impact the nesting behaviours/capabilities of smaller, presumably less dominant, females.

Wild crocodile populations have demonstrated resilience by adapting to multiple climate changes over many years. Current changes in climate are largely driven by human activities and are occurring faster than in the past, with largely unpredictable outcomes. If climatic changes in nesting environments occur, female crocodiles might reduce their nesting activities, purposefully alter the timing and/or depths of their nests or be forced to compete for desirable or thermally optimal nesting sites. However, such compensations have been found to be insufficient in some other species, including nesting lizards, sea turtles and American alligators (Telemeco et al., 2009; Hill et al., 2015; Bock et al., 2020), suggesting that similar limitations could arise for Nile crocodiles. Identifying the features making nesting sites "preferable" to farmed crocodiles (considering both thermal and behavioural effects) will inform future pen layout/alteration requirements, ensuring welfare requirements are met. Nest site preferences are complex but quantifiable, and therefore manageable on farms.

Linking prior research to the hypotheses tested here is difficult, not only are former studies focussed on wild crocodiles whose nesting experiences vary from those of farmed crocodiles, but this was also a thermal environment and nesting behaviour assessment rather than an incubation temperature assessment. Even without eggs present, this type of study can reveal how crocodiles interact with their environment during the nesting season, enabling the identification of factors positively influencing nesting behaviours, strategies, and possibly nesting success in farmed settings. The roles that section, orientation, human presence, ambient/environmental temperatures, and substrate temperatures play in determining nest site selection and nest depths on farms, require further evaluation. Assessing multiple nesting groups (ideally alongside individual identifications), over multiple nesting seasons, with more nests, including further climate variables, and adding nighttime recordings will benefit future studies. These findings contribute to our understanding of the critical influence of temperature on the thermal profiles within selected nesting sites and also nesting Nile crocodile behaviours, affording insights and methodological refinements for future ecological and conservation studies of this complicated topic.

## Ethical committee/institutional review board (IRB) approval

Ethical approval for this study was granted by the University of Pretoria Animal Ethics Committee (NAS327/2020).

## CRediT authorship contribution statement

**Devon Viljoen:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Edward Webb:** Writing – review & editing, Formal analysis, Conceptualization. **Jan Myburgh:** Writing – review & editing, Conceptualization. **Christoff Truter:** Writing – review & editing, Conceptualization. **Hannes van Wyk:** Writing – review & editing. **Albert Myburgh:** Writing – review & editing, Investigation.

## Data accessibility statement

Due to a confidentiality agreement with the farm involved, the datasets related to this article are not readily available.

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## Declaration of competing interest

None.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2025.104179>.

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