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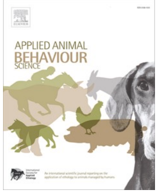

Adaptive thermal responses of captive Nile crocodiles (*Crocodylus niloticus*) in South Africa

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ABSTRACT

The current study assessed the ambient temperatures, and those selected, by captive adult Nile crocodiles on a commercial farm in South Africa. Non-invasive data capture techniques were developed to ensure the crocodiles natural behaviours were not disrupted or altered. Thermal and climate data, over summer and winter seasons, were collected from local weather stations, an on-site Internet of Things system, and a Mavic 2 Enterprise Dual drone. The method developed in this paper transformed relative thermal maps (produced by a DJI Mavic 2 Enterprise Dual drone) into a predictive model in which temperatures were derived to within 2.6°C per pixel of a processed orthophoto. Crocodile thermal and behavioural data were extracted from the drone imagery and juxtaposed with climate and thermal data from the pen. The greatest number of crocodiles were counted during early morning winter flights and the lowest number during late afternoon summer flights. Material (concrete, water, nest, grass/sand) selection by crocodiles varied with season, time of day and daily climatic conditions. Crocodile back temperature (10.2–49.6°C, $\mu = 30.4$°C) ranges fell within those of their positional/environmental (10.6–66.6°C, $\mu = 28.7$°C) temperature range selections. Strong, positive, significant correlations were found between crocodile back temperatures and positional temperatures for both winter and summer seasons, highlighting ectothermy. Application of this methodology on a commercial crocodile farm facilitated the inspection of potential shortfalls of the pens design from a thermal perspective, as well as suggestions for improvements that would ameliorate crocodile thermal discomfort (relating to hyperthermia).

1. Introduction

Intensive communal pens in commercial crocodile farming are ubiquitous (Bothma and Van Rooyen, 2005), and there are a multitude of pen layouts within and across farms that facilitate husbandry practices, maintain production outputs and optimize growth, survival, skin quality, and disease control (Bolton, 1989; Bothma and Van Rooyen, 2005; Verdade et al., 2006). In addition to facilitating production, the artificial environment created by a pen determines animal welfare, particularly with respect to thermal requirements. As ectotherms, crocodilians rely on environmental temperatures to maintain a "favourable" or "preferred" range of body temperatures (T_b), which influences health, appetite, and metabolic rates (Lang, 1987a; Huchzermeyer, 2003; Bothma and Van Rooyen, 2005; Bassetti et al., 2014).

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Crocodilians achieve and maintain a preferred T_b by selecting appropriate environmental temperatures, either seeking or avoiding heat by engaging in specific thermal behaviours (Lang, 1987b; Huchzermeyer, 2003; Downs et al., 2008). Body temperatures differ among individuals and species, and are functions of nutritional or reproductive status, climatic conditions, social interactions, and ontogeny (Lang, 1987b; Seebacher and Grigg, 2001; Telemeco and Gangloff, 2021).

For intensive crocodilian farming, recommended ambient temperatures within pens range between 17 °C and 35 °C (Bolton, 1989; Bothma and van Rooyen, 2005; Bassetti et al., 2014). Recommendations for optimal production and fitness tend toward the higher end of this range (Seebacher and Grigg, 2001; Huchzermeyer, 2002; Seebacher, 2005). Air temperature, humidity, solar radiation, windspeed and water temperature all play a role; and this is incorporated into pen design features such as shading, water to land ratios, and floor materials where the crocodiles will spend much of their time basking (Lang, 1987b; Bolton, 1989; Huchzermeyer, 2003; Downs et al., 2008; Crocodile Farmers Association of Zimbabwe (CFAZ): Codes of Practice, 2012). For younger crocodiles, strict temperature controls are essential in intensively managed environments, while breeder crocodiles in natural pens experience ambient temperatures dictated by the prevailing local climate (Bolton, 1989; Huchzermeyer, 2003; Bothma and Van Rooyen, 2005; Downs et al., 2008; Crocodile Farmers Association of Zimbabwe (CFAZ): Codes of Practice, 2012). Continuous ambient temperatures between 10°C and 20°C suppress feeding behaviours for multiple reptilian species, while consistent and unavoidable ambient temperatures exceeding 35°C are considered lethal (Colbert et al., 1946; Lang, 1987b; Bolton, 1989; Huchzermeyer, 2002). In addition to immediate environmental temperatures, optimal core T_b between 28°C and 33°C are recommended for crocodilians (Colbert et al., 1946; Huchzermeyer, 2003; Crocodile Farmers Association of Zimbabwe (CFAZ): Codes of Practice, 2012). When optimizing pen climates, humidity levels of 60–90% have been suggested in controlled farming environments (such as those for raising hatchlings). In contrast, natural pens, such as those for breeding groups, are subject to the local ambient humidity (Terpin et al., 1979; Davis, 2001; Downs et al., 2008).

Exceeding the acceptable ranges of farm temperatures and humidities can serve as significant stressors. Intensive crocodile farms have experienced hyperthermia-related mortalities in southern Africa, particularly during warmer months (Personal communication: Prof J.G. Myburgh, Exotic Leather Research Centre, University of Pretoria). In South Africa, the NSPCA (National Society for the Prevention of Cruelty to Animals) issued warnings in respect of environmental temperatures for intensively farmed crocodiles, emphasising the need for effective shade provision and maintaining water temperatures below air temperatures in summer, especially in shallow ponds that are not regularly replenished (Personal communication: Prof J.G. Myburgh).

In communal pens, how crocodiles behave affects production and survival. Often, a social hierarchy forms where dominant animals dictate feeding areas or restrict access to certain areas (Lang, 1987a; Morpurgo et al., 1993; Brien et al., 2013a, 2013b). Agonistic behaviours ensue which can increase stress levels; poor management and increasing temperatures influence crocodile aggression (Pooley et al., 2019). Social interactions that prevent subordinate individuals from maintaining optimal T_b likely influence growth and size (Grigg et al., 1998; Seebacher and Grigg, 2001; Verdade et al., 2006; Brien et al., 2013a, 2013c; Bassetti et al., 2014). Management of density, feeding, size classes and available thermal gradients is therefore important when farming crocodilians (Lang, 1987a; Morpurgo et al., 1993; Manolis and Webb, 2016).

Crocodilian thermoregulatory behaviours include basking, gaping, shuttling, thermal posturing, and occasional burrowing during temperature extremes (Lang, 1987a; Seebacher and Grigg, 2001; Manolis and Webb, 2016; Price et al., 2022). Crocodilians use diurnal basking to elevate T_b with minimal effort/energy costs (Seebacher, 2005; Downs et al., 2008). Behavioural assessments should encompass as many aspects of both social and maintenance behaviours as possible (Brien et al., 2013a, 2013b, 2013c), and should be considerate of the animals so as not to alter behaviours. Monitoring temperatures in larger ectotherms is complicated by their size and movement between land and water (Lang, 1987b; Downs et al., 2008; Bassetti et al., 2014). The monitoring of thermal environments and behaviour of crocodiles have therefore been limited, although recent advances in drone technology enable novel and non-invasive methodological approaches.

This study presents a method for the derivation of thermal landscape maps using the DJI Mavic 2 Enterprise Dual, combined with open-source photogrammetry and GIS software (ODM version 1.9.3 build 30, and QGIS version 3.16-Hannover). The derived method, in conjunction with local weather station data and an Internet of Things (IoT) system of loggers, was used to monitor the thermal environment, temperature selections and behaviour of breeder Nile crocodiles in a current commercial farm setting in South Africa.

2. Materials and methods

2.1. Ethics

Ethical approval for this study was granted by the University of Pretoria Animal Ethics Committee, reference number NAS327/2020.

2.2. Animals, husbandry, and pen layout

A large breeder pen (5020 m^2) on a commercial crocodile farm in South Africa was monitored for this study. The pen housed 233 crocodiles ranging in snout-hindlimb lengths from 1.2–2.4 m (measured according to the methodology of Viljoen et al., 2023), with an approximate sex ratio of 1 male to 4.5 females. The crocodiles studied had been housed in the same enclosure since the early to mid-1990s, experiencing consistent rearing in terms of diet, housing, and general animal husbandry prior to this study. The standard pen setup was not altered further than the placement of LoRaWAN (Low-power wide-area network) loggers. Logger placement occurred over a one-day period, a month before any flights were conducted, with the assistance of farm personnel. The farms regular feeding and cleaning schedules remained unchanged for the trial. Diets were also not modified so as not to stress the crocodiles or alter their regular behaviours. To maintain the comfort and socialization activities of the crocodiles, the personnel attending the trial pen were kept consistent. The pen contained a section of walkway from a neighbouring tourist centre. All drone flights were conducted on weekdays to ensure no tourists were present during the flights. The pen contained, and was divided up by, four main areas or material types: water, concrete, grass/sand, and nests. There were three water bodies within the pen, each surrounded by areas of concrete. The water bodies have a maximum depth of 2 m, and water levels are maintained year-round. There were also several areas that were a mix of sand and grassy patches, the ratio of these two material types varied with season and so for ease of analysis this area type will be referred to as grass/sand in the current study. Sections of the pen were cordoned using low brick walls and were filled with river sand. Crocodiles typically use these areas for nesting, and these will henceforth be referred to as “nests” to avoid confusion with sandy areas in the pen that are not used for nesting. Within the pen, shading was provided by scattered trees, a shade net, and pen perimeter walls, with the extent of shading varying depending on the time of day.

2.3. UAV surveys

2.3.1. Aerial image acquisition

Uncrewed aerial vehicle (UAV) data was captured over four days, two summer days (26 January 2022 and 3 February 2022) and two winter days (12 August 2022 and 15 August 2022). Daily climatic condition was also noted, 26 January 2022 and 15 August 2022 were cool days (relatively) within their seasons, and 3 February 2022 and 12

August 2022 were warm days (relatively) within their seasons. Flights began in the morning and were conducted hourly, with a minimum of 8 flights per day. The data were divided into morning and afternoon timeslots, based on the flights conducted, as follows: early morning between 07:30 and 09:59 AM, late morning between 10:00 and 11:59 AM, early afternoon between 12:00 and 13:59 PM, and late afternoon between 14:00 and 15:59 PM. For each flight ($n = 33$), a DJI Mavic 2 Enterprise Dual drone was flown on the same automated flight path using a 3rd party flight software package (Dronelink) at an altitude of 35 m with 85% side and frontal image overlap. The UAV covered an area of approximately 15000 m^2 in 9 minutes. Between flights, all equipment was kept in an air-conditioned room (22°C) to minimize drift from overheating of the uncooled thermal sensor, ensuring the starting temperature of the UAV was constant.

Six GCPs (ground control points) were distributed along the perimeter of the pen. The GCPs used in this study were inexpensive square polystyrene platforms (60 cm x 60 cm) covered with aluminium foil and black paint as per Messina and Modica (2020). Aluminium foil has an emissivity of 0.03, creating sufficient contrast with black paint and adjacent pen materials, making it easily recognizable in thermal images (American Society of Heating, Refrigerating and Air-conditioning Engineers, 2009; Messina and Modica, 2020). The GCPs were systematically positioned in predetermined positions around the perimeter of the pen for each flight, ensuring precise georeferencing of the resulting orthophotos based on established geospatial calibration methodologies.

2.3.2. Thermal mapping settings and workflow

The DJI Mavic 2 Enterprise Dual drone does not store the absolute temperature associated with the long wave infrared measurements captured by its thermal sensor. The DJI Pilot 4 interface was used to specify a greyscale colour palette, providing a linear conversion of thermal data (thermal range set between 5°C and 65°C) to RGB variables (between 0 and 255; where, using the greyscale colour palette results in equal colour values within all three colour bands) which were stored in the jpeg files associated with the thermal sensor. During flight, but not within the perspective of the UAV, a handheld thermometer (*ASSTech* Process Electronics and Instrumentation handheld infrared thermometer, *ST653*) was used to measure the temperature of homogenous areas representing various materials outside the perimeter of the pen (and not within view of the crocodiles), with the thermometer emissivity set to 0.94 (as per the instruction manual for the materials under study i.e., concrete, brick, water, soil). The distance from the thermometer to the materials measured was maintained at 1 m for all measures. Temperatures recorded by the thermometer were then used to elucidate the temperatures associated with the colour band value outputs of the resulting thermal orthophotos (Eq. 1).

2.3.3. Thermal image processing settings in ODM and QGIS

Processing parameter testing for the derivation of orthophotos from thermal images in ODM resulted in the selection of settings which differ from the standard “high resolution” option in the following ways: orthophoto resolution was set to the ground sampling distance (GSD) of the original images (11.16 cm/pixel in this case), and the lens selection was set to fisheye. RGB images were processed using the “default” settings in ODM with orthophoto resolution set to the GSD associated with the RGB images (1.42 cm/pixel). An Emlid reach RS+ differential GPS was used to mark the position of each ground control point and all images therefore align after photogrammetric processing. Where misalignment occurred, georeferencing was performed in QGIS using a linear conversion through a thin-plate spline projection to resize and georeference each image into the correct position. Once the thermal images were aligned, the thermal orthophoto data was preserved as RGB image data ranging from 0 to 255 across the three colour bands. The following steps were followed to convert RGB thermal orthophotos into relative temperature maps:

1. Using the point creation tool in QGIS, a marker was placed at each location where temperature measurements were recorded with the handheld thermometer during flights.
2. Using the sample raster tool in the processing toolbox, the RGB data was derived from the thermal layer at each of the points across all thermal orthophotos.
3. The sampled points data was then exported to a spreadsheet, where the three RGB band values were averaged into a separate column. The measured temperatures taken with the handheld thermometer during flights were added next to the averaged RGB values.
4. A linear relationship was fitted to these two variables and an equation describing the relationship was derived.
5. A new relative temperature map of the area under survey was created for each flight using the raster calculator in QGIS, where the RGB values of the thermal orthophotos were set as x in the derived equation.

2.4. The thermal environment

A LoRaWAN system recorded hourly ambient temperature, various material temperatures and humidity throughout the pen. The system consisted of a router (LtAPHD LR8 3xSIM2xmPCIe Wi-Fi LTE Router), antenna (a LoRa 6.5dBi Antenna kit with 1 m SMAF), humidity and temperature sensor (SenseCAP LoRaWAN Wireless Air Temperature and Humidity Sensor; placed in a permanently shaded area), and small temperature sensors (LHT65 LoRaWAN Temperature and humidity sensor). The router and antenna were placed close to the pen in a room with a reliable Wi-Fi connection. The SenseCap sensor recorded hourly ambient temperatures and humidity. The LHT65 sensors recorded hourly concrete temperatures in sunny and shaded areas of the pen, and 30 cm deep water temperatures. Accuracy configurations, data collection and data visualization for the LoRaWAN loggers were obtained via a dashboard provided by Ubidots (https://ubidots.com/). South African Weather Service data (ambient temperature, relative humidity, windspeed) and Weather Underground data (radiation) were incorporated into the study to supplement that of the LoRaWAN system.

2.5. Extracting crocodile behaviour and environmental/temperature selection data

Data were extracted from the resulting processed imagery using point and polygon layers in QGIS (version 3.16 Hannover). Point layers were used to attain temperature measurements for the back of each crocodile and the position of the crocodile. This was accomplished by placing a point layer marker centrally on the back of each crocodile in view and another point layer marker next to the crocodile on the material the crocodile was selecting. If a crocodile was positioned over two material types, the point was placed on the primary material type the crocodile was occupying. Back temperatures and the corresponding selected positional temperatures were compared across season, allowing the assessment of the thermal options selected by these captive crocodiles. A regression analysis was also performed to deduce the accuracy with which these temperatures could be inferred from one another. A polygon layer was used to distinguish areas of the pen based on material type. Each material was outlined with the polygon layer tool and numbered; perimeter and area information were also extracted with this layer type. Crocodile material selections and use of the various pen areas/materials (water, concrete, nests, grass/sand) were assessed per time of day and season to deduce thermoregulatory behaviours.

Heat avoidance and heat seeking behaviours were intuited from the crocodiles back temperatures relative to those of the materials they were selecting. When the temperature of the crocodile’s back was lower than that of the selected material, this was designated as "heat seeking" behaviour. Conversely, if the temperature of the crocodile’s back was higher than that of the material the crocodile was selecting, this was designated as "heat avoidance” behaviour. In cases where the two corresponding temperatures were equal, no thermal behaviour was inferred. It was assumed that crocodile behaviours would be primarily driven by temperature, to avoid confounding the findings, the assessments occurred externally to the breeding season and to feeding/ cleaning days. It is important to note that crocodile back temperature was used as an approximate indicator of the body temperature of the crocodile, but it is not equivalent to the core temperature or deep body temperature of the crocodiles under consideration. Rather, a crocodile's back temperatures provided a thermal value for direct comparison with the surface temperature of the substrate upon which it was positioned.

2.6. *Statistical analyses*

The data for this study were analysed in R (2022.12.0 Build 353) and IBM SPSS Statistics (version 28). A multivariate analysis of variance, two tailed partial correlations, Chi square, and regression analyses were performed. Bonferroni corrections were applied to post-hoc pairwise comparisons. Differences between variable means were analysed for the determination of significant differences at $P < 0.05$.

3. Results

3.1. *Thermal map conversions*

The relationship between temperature measurements taken with the handheld thermometer ($n = 330$) and colour information from the RGB bands ($n = 330$) of the processed thermal orthophotos could be described through Eq. 1:

$$y = 0.3593x + 5.16 \ (R^2 = 0.9454; P < 0.001), \quad (1)$$

where y = temperature of the selected pixel, and x = average extracted value of the three RGB bands with an average absolute error of 2.06 ± 1.32ºC, and a Root Mean Squared Error of 2.6ºC.

3.2. *The thermal environment*

Hourly ambient temperatures and relative humidity from the closest national weather station (SAWS) are depicted in Fig. 1. Ambient temperatures and relative humidity data during the flights ranged from 10.6–35.3°C and 18.6–61.7% humidity, respectively. Ambient temperature varied significantly with season ($P < 0.001$, $F = 19371$, $df = 1$) and had significant effects on crocodile back temperatures ($r = 0.28$, $P < 0.001$) and positional temperatures ($r = 0.23$, $P < 0.001$). Relative humidity varied significantly with season ($P < 0.001$, $F = 12771$, $df = 1$) and had significant effects on crocodile back temperatures ($r = -0.38$, $P < 0.05$) and positional temperatures ($r = -0.31$, $P < 0.05$).

Windspeed (SAWS) ranged from 0.0 to 3.6 m/s throughout the flight periods, with a mean of 0.8 m/s (1.2 m/s in summer, and 0.4 m/s in winter). Windspeed varied significantly with season ($P < 0.001$, $F = 906.6$, $df = 1$) and had a significant effect on crocodile back temperatures ($r = 0.27$, $P < 0.001$) and positional temperatures ($r = 0.21$, $P < 0.001$). Radiation (Wunderground) ranged from 65.0 to 952.3 W/m^2 throughout the flight periods, with a mean of 489.3 W/m^2 (487.1 W/m^2 in summer, and 490.9 W/m^2 in winter). Although the radiation did not vary significantly between summer and winter seasons ($P = 0.42$, $F = 0.66$, $df = 1$), it did have a significant influence on crocodile back temperatures ($r = 0.22$, $P < 0.001$) and positional temperatures ($r = 0.18$, $P < 0.001$).

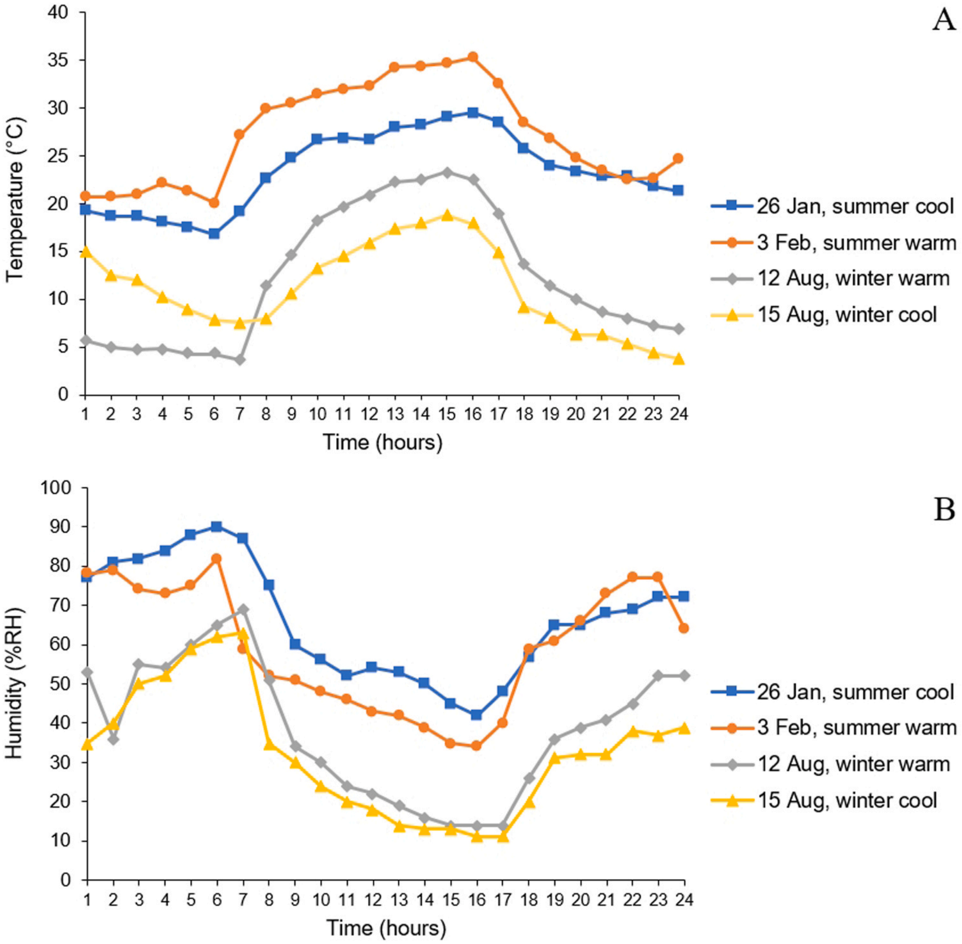

Fig. 1. Hourly ambient temperature (A) and relative humidity (B) for the four days included in the assessment.

Water temperatures varied significantly between summer and winter seasons ($P < 0.001$, $F = 4377$, $df = 1$) and had a significant effect on crocodile back temperatures ($r = 0.36$, $P < 0.001$) and positional temperatures ($r = 0.28$, $P < 0.001$). Sunny concrete temperatures varied significantly between summer and winter seasons ($P < 0.001$, $F = 4106$, $df = 1$) and had a significant effect on crocodile back temperatures ($r = 0.35$, $P < 0.001$) and positional temperatures ($r = 0.28$, $P < 0.001$). Shaded concrete temperatures varied significantly between summer and winter seasons ($P < 0.001$, $F = 6556$, $df = 1$) and had a significant effect on crocodile back temperatures ($r = 0.22$, $P < 0.001$) and positional temperatures ($r = 0.16$, $P < 0.001$). Fig. 2 depicts the water and concrete (sunny and shaded) temperatures recorded by the LoRaWAN loggers. Daily climatic condition, between seasons and within each season, significantly affected water and concrete temperatures ($P < 0.001$).

3.3. *Crocodile thermal behaviour and pen/material utilization*

The proportional layout of the pen calculated from UAV imagery was as follows: water bodies 22.5%, nests 19.1%, concrete 26.2% and grass/sand 32.2%. The number of crocodiles visible from the UAV imagery during each flight varied from 111 to 233. An average of 151 crocodiles could be viewed in the imagery captured during the summer flights, compared to an average of 214 crocodiles captured during winter flights. Both time of day and season were significant ($P < 0.001$, $\chi^2 = 2607.5$, $df = 96$) determiners of the number of crocodiles counted, with the greatest number of crocodiles counted during the early morning winter flights and the lowest during late afternoon summer flights. The proportion of crocodiles located on the various materials during each set of flights are plotted in Fig. 3. Daily climatic condition and season both had a significant effect on the proportional use of the material types within the pen ($P < 0.001$, $\chi^2 = 2017$, $df = 9$).

To assess thermal behaviour, the crocodile back temperatures and corresponding positional temperatures were compared, and two behaviours were inferred. The first was "heat seeking" (i.e., attempting to warm up), and the second was "heat avoidance" (i.e., attempting to cool down). A Generalized Linear Model Analysis revealed these thermal behaviours were significantly affected by ambient temperature, relative humidity, water temperature, windspeed, radiation, and sunlit-concrete temperatures (all $P < 0.001$ except radiation which had $P = 0.003$). Time of day, season, and daily climatic conditions all significantly ($P < 0.05$) affected thermal behaviours expressed. The proportions of the behaviours expressed in winter varied significantly with time of day ($P < 0.001$, $\chi^2 = 102.3$, $df = 3$), specifically between early morning and all other times of the day. In summer, the proportions of the behaviours expressed varied significantly ($P < 0.001$, $\chi^2 = 22$, $df = 3$) between early morning and early afternoon and late afternoon, with early afternoon behaviours also varying from late morning behaviours.

Crocodile back temperatures and positional temperatures varied significantly with thermal behaviours ($P < 0.001$, $F = 241.7$, $df = 1$; and $P < 0.001$, $F = 5762.8$, $df = 1$, respectively). Incorporating season into these models showed that it too exhibited a significant effect on crocodile back temperatures ($P < 0.001$, $F = 133.7$, $df = 1$) and positional temperatures ($P < 0.001$, $F = 176.2$, $df = 1$). All pairwise comparisons of crocodile back temperature, across behaviour within each season, as well as across seasons within each behaviour, differed significantly (all $P < 0.001$). All pairwise comparisons of positional temperature across behaviour within each season, as well as across seasons within each behaviour, also differed significantly (all $P < 0.001$).

The thermal behaviours exhibited varied significantly ($P < 0.001$, $\chi^2 = 1190$, $df = 3$) between the materials selected by the crocodiles, this held true for both summer ($P < 0.001$, $\chi^2 = 719.5$, $df = 3$) and winter ($P < 0.001$, $\chi^2 = 1084.3$, $df = 3$) seasons. Fig. 4 shows the proportional behaviours exhibited per material type for summer and winter seasons. The selected materials, in order of most to least frequented, for cooling behaviours in the summer were water> nests> grass/sand> concrete. The selected materials, in order of most to least frequented, for heating behaviours in summer were the opposite of the cooling materials order for that season. Winter material selections, in order of most to least frequented, for cooling behaviours were water> concrete> nests> grass/sand. The selected materials, in order of most to least frequented, for heating behaviours in winter were again reversed for that season.

Where intuited behaviours were non-conclusive (i.e., constituting neither heating nor cooling activities) the proportions of this "neutral" temperature state were spread over the pen materials in the following selections: 82% water bodies, 10% concrete, 6%grass/sand areas, and 2% nest areas. Only 3.4% of all the crocodiles measured for this study fell into this "neutral" temperature category.

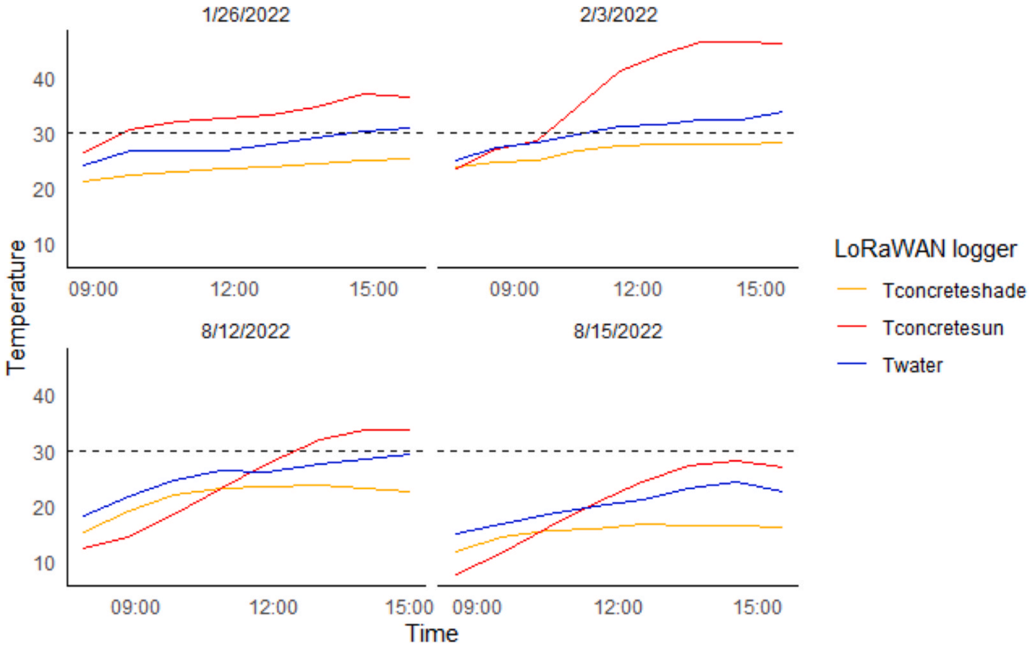

Fig. 2. LoRaWAN water and concrete (shaded and sunny) temperatures within the timespan of the flights. All plots contain a dashed line at 30°C for reference.

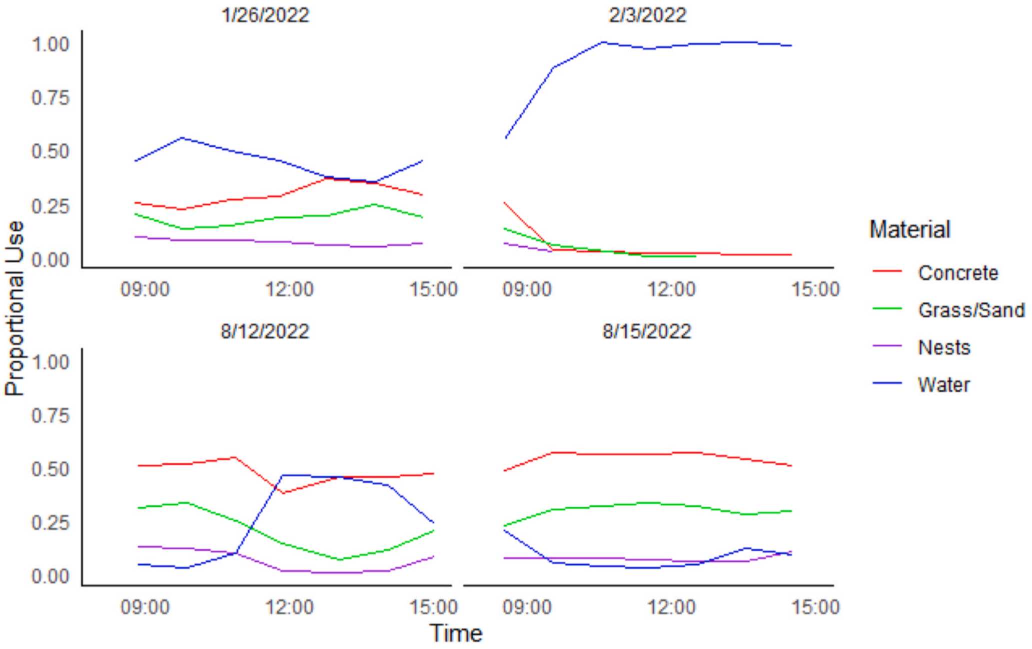

Fig. 3. Hourly proportional material use within the pens for all flights.

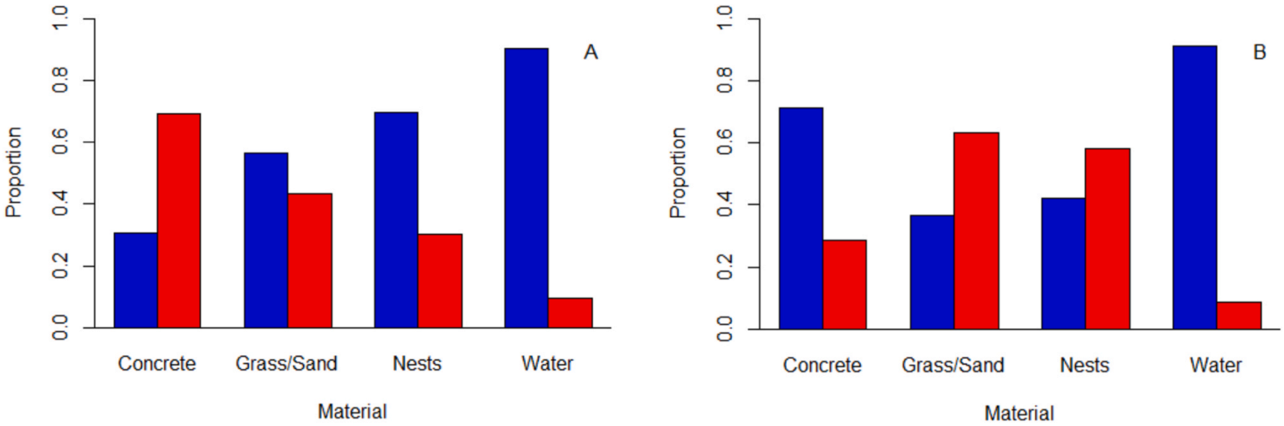

Fig. 4. The proportions of heat avoidance (blue) and heat seeking (red) behaviours per material type in summer (A) and winter (B) seasons.

3.4. Crocodile environmental/temperature selections

Crocodile back surface temperatures over all flights and seasons ranged from 10.2 to 49.6°C, with a mean of 30.4°C. The positional temperatures selected by the crocodiles over all flights ranged from 10.6 to 66.6°C, with a mean of 28.7°C. Crocodile temperatures in winter ranged from 10.2–49.6°C (μ = 29.9°C), whilst in summer crocodile temperatures ranged from 20.6–47.0°C (μ =31.1°C). Positional temperature selections ranged from 20.6–66.6°C (μ = 29.3°C) in summer and from 10.5–55.9°C (μ =28.2°C) in winter. Crocodile back temperature and positional temperatures varied significantly with daily climatic condition ($P < 0.001$, $F = 88.7$, $df = 1$, and $P < 0.001$, $F = 66.6$, $df = 1$, respectively). Mean hourly crocodile back temperature and corresponding positional temperatures are plotted per season and daily climatic condition in Fig. 5.

Positional temperatures selected by the crocodiles in this study are tabulated (Table 1) for seasons and material types available within the pen. These temperatures were all derived from UAV imagery, and the water temperatures reflect only the surface-water temperatures. Positional temperatures were significantly affected by material selection ($P < 0.001$, $F = 767.4$, $df = 3$) and season ($P < 0.001$, $F = 806.1$, $df = 1$). In summer, positional temperature selections varied significantly between all material types (all $P < 0.001$, except nests and grass/sand where $P = 0.004$). In winter, this variation remained significant (all $P < 0.001$) except between grass/sand and nests ($P = 0.86$).

Crocodile back temperatures in this study are tabulated (Table 1) for the seasons and material types available within the pen. Crocodile back temperatures were significantly affected by material selection ($P < 0.001$, $F = 176.2$, $df = 3$) and season ($P < 0.001$, $F = 582.1$, $df = 1$). In summer, back temperatures of crocodiles in the water varied significantly from back temperatures of crocodiles occupying all other material types (all $P < 0.001$). There was no significant variation between back temperatures of crocodiles occupying concrete, nests, or grass/sand areas in this season. In winter, the back temperatures of crocodiles occupying water bodies varied significantly from those occupying other materials (all $P < 0.001$); however, there was also a significant difference in back temperatures of crocodiles occupying concrete and grass/sand areas ($P = 0.045$). Back temperatures of crocodiles occupying nests in winter did not vary significantly from those of crocodiles occupying concrete or grass/sand areas of the pen ($P = 0.46$).

A curve estimation analysis in SPSS confirmed that the relationship between crocodile back temperatures and positional temperatures was

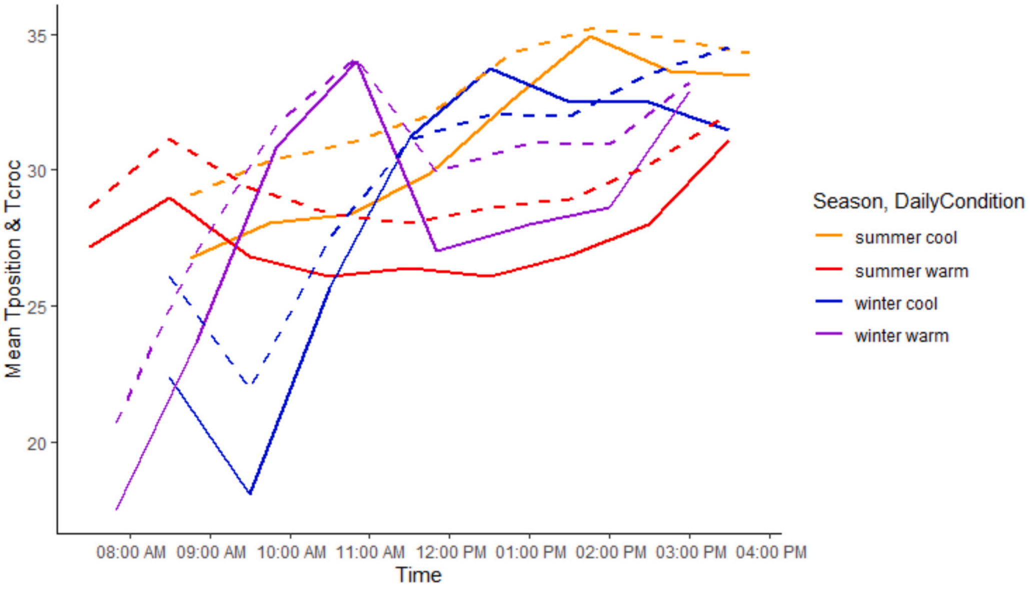

Fig. 5. Mean hourly crocodile back temperatures (Tcroc, represented by dashed lines) and positional temperatures (Tposition, represented by solid lines) are plotted against time (corresponding to all flights on each date). Both season and daily climatic condition are accounted for in the graph's coloration.

Table 1
Descriptive statistics (minimum, maximum, mean, and standard deviation) of positional temperature (°C) data (first half of the table) and crocodile back temperatures (second half of the table) per material type and season.

Material	Summer				Winter			
	Min	Max	Mean	sd	Min	Max	Mean	sd
Concrete	23.1	57.0	36.9	5.8	10.5	49.1	25.9	7.0
Grass/sand	20.7	53.0	32.9	7.2	13.4	55.9	35.3	9.1
Nests	20.6	66.6	31.3	9.7	13.5	54.1	35.6	10.3
Water	21.1	33.5	26.1	1.9	10.5	27.4	19.1	2.8
Concrete	23.1	47.0	34.4	3.6	11.3	43.6	30.1	5.3
Grass/sand	22.8	43.6	33.7	3.9	15.6	49.6	31.5	5.4
Nests	20.6	43.4	33.7	5.3	13.9	45.5	31.0	6.6
Water	22.2	40.7	29.4	3.7	10.2	37.9	25.6	6.0

best modelled by an S-curve, the resulting equation is presented in Eq. 2. Eq. 3 describes the relationship when exclusively summer data was assessed, and Eq. 4 when exclusively winter data was assessed.

$$T_{croc} = e^{\left(3.861+\left(-12.223/T_{position}\right)\right)},\ (R^2 = 0.54;\ P < 0.001) \qquad (2)$$

$$T_{croc} = e^{\left(3.982+\left(-15.652/T_{position}\right)\right)},\ (R^2 = 0.44;\ P < 0.001) \qquad (3)$$

$$T_{croc} = e^{\left(3.842+\left(-11.745/T_{position}\right)\right)},\ (R^2 = 0.57;\ P < 0.001) \qquad (4)$$

Fig. 6 depicts the relationship between crocodile back temperatures and the corresponding positional temperatures that the crocodiles were selecting for both summer and winter seasons. Correlation coefficients of $r = 0.64$ ($P < 0.05$) in summer and $r = 0.70$ ($P < 0.05$) in winter indicate a strong positive relationship between the two variables for both seasons.

4. Discussion

4.1. Low-cost thermal mapping

The methodology described here is a cost-effective alternative to more expensive proprietary software and larger UAV platforms, as well as a less invasive approach to temperature assessment via monitoring external body temperatures directly. For the current study, it provided sufficient resolution for distinguishing the thermal features of the respective breeding and basking areas for crocodiles on a commercial farm. This method could be used to identify suboptimal thermal regimes which may be detrimental to crocodile welfare. We envisage the broad scale use of this approach for hotspot detection in commercial settings. An important feature of raster data means that it can be easily mathematically manipulated and can be partitioned to identify specific areas of interest. It can be used to detect changes in critical parameters and/or to identify areas requiring further investigation, saving analytical time and costs.

4.2. Crocodile thermal behaviour and pen/material utilization

The average number of crocodiles visible per season and time of day can be attributed to thermoregulatory activities/behaviours. Even within a season, the changing daily thermal regimes vastly affected the crocodile's selection of an appropriate micro-environment. For example, on a warm summer day, ≥ 85% of the crocodiles in view selected water between 09:30 AM and 15:30 PM. The land temperatures in the pen were seemingly too hot, and the water body became the only refuge from these temperatures. Wild crocodiles similarly utilize aquatic environments extensively during the summer season, shuttling between land and water to thermoregulate their body temperatures. A potential welfare issue in commercial crocodile farming practices is the density of the population being confined to limited aquatic spaces, necessitating aggregation to mitigate overheating. Wild crocodiles can spatially distribute themselves, maintaining thermoregulation activities while simultaneously maintaining individual spacing. Farmed crocodiles do not necessarily have this same distribution opportunity. Consequently, the provision of sufficient thermal gradients (e.g., increased shaded areas within the pen during the summertime) on land, and over waterbodies, may be an effective alternative from both a thermoregulatory and social perspective.

With fewer crocodiles captured in the summer imagery; the assumption could be made that the uncaptured crocodiles missing from the imagery were also occupying the water bodies or shaded regions of the pen and were therefore out of sight. Overall, warmer summer temperatures resulted in the crocodiles exercising a greater degree of heat avoidance behaviours by retreating to the water. Conversely, the cool winters day showed ≤ 12% of the crocodiles in view selecting water bodies between 09:30 AM and 15:30 PM. For this seasonally cool day in

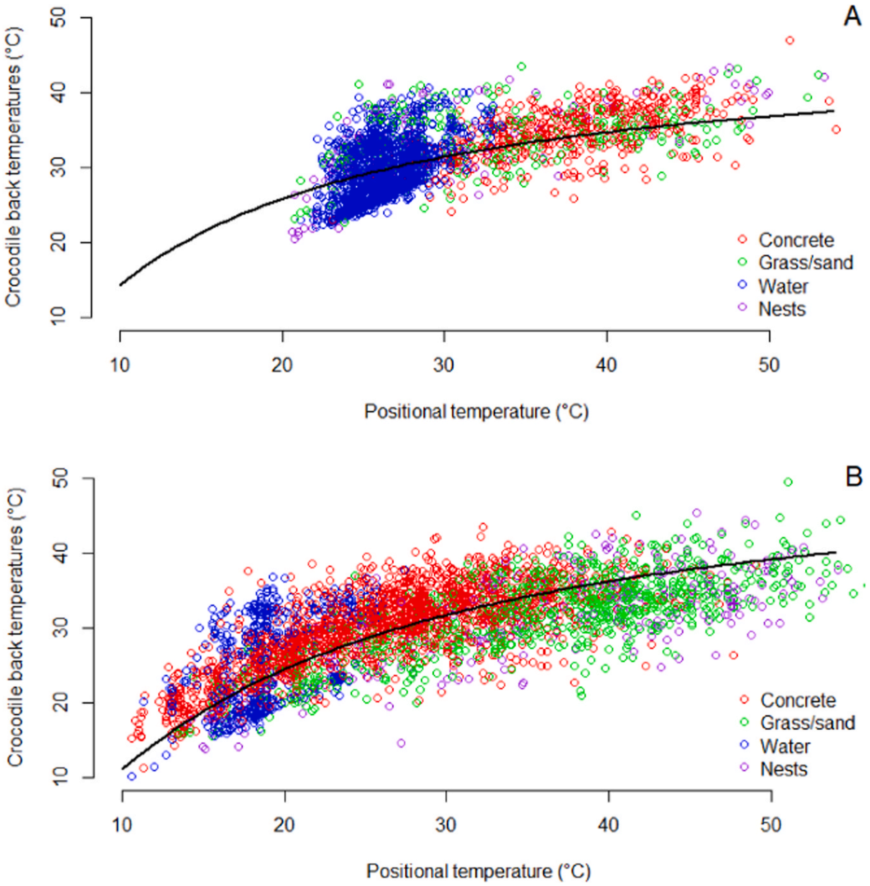

Fig. 6. The relationship between crocodile back temperature and positional temperature selected by the crocodiles, for summer (A) and winter (B) seasons. The colouration of the plot indicates which material type the crocodiles were selecting for each datapoint.

winter, water temperatures were "too cool", and the land areas were preferred by the crocodiles. Overall, cooler winter temperatures resulted in the crocodiles exhibiting heat seeking behaviour via basking on land areas where these materials functioned as heat sources as the day warmed up. Of the four pen materials assessed, the sandy nesting areas were the least frequented material type. This area comprised close to a fifth of the total pen area, and a quarter of the total land-area available to the crocodiles, yet only 6.75% of the crocodiles utilized this area over all seasons and timeslots.

Significant variation in heat seeking and heat avoidance behaviours between the early morning timeslot and all other timeslots was likely due to the thermal properties of the pen materials, with land-based materials acting as heat sources once they had accrued enough warmth, and the water bodies acting as heat sinks (Lang, 1987a). Once the land temperatures warmed sufficiently, the crocodiles basked from late morning, which concurs with previous Nile crocodile basking assessments (Downs et al., 2008).

Although there is a general lack of confirmation regarding the exact thermoregulation link to cardiac shunting (Grigg and Alchin, 1976; Hicks, 2002; Seebacher and Franklin, 2004; Porter et al., 2016), it is possible that partially submerged crocodiles may have been thermally "shunting" heat received through the peripheral parts of the body that were in direct sunlight (note: to be captured for analysis in this study, a portion of the crocodile, either the back or the head, had to be visible within the water body), directly into the water. For the "neutrally" behaving crocodiles this could explain the maintenance of back temperatures closely matching those of the water bodies they were selecting. Alternatively, the thermal camera resolution may not have been able to capture the variation between the portion of the crocodile's body visible to that of the water surrounding the animal. It is also possible that the surface temperature of the crocodile when wet would reflect that of the water because the animal may have submerged recently.

4.3. Crocodile environmental/temperature selections

The crocodiles maintained back temperatures within a narrow/restricted range, relative to the wide range of environmental/material temperatures available. Apart from area/material selections (via shuttling between land and water) and climate conditions, physiological processes (cutaneous vasodilation/vasoconstriction and altered heart rates) and thermoregulatory behaviours (gaping and posturing) may also have contributed to the crocodile's back/body temperature ranges (Grigg and Alchin, 1976; Seebacher, 1999; Hicks, 2002; Porter et al., 2016). The variation between environmental and crocodile back temperatures suggests that even when seasonal climatic factors are considered, crocodiles were consistently able to maintain back temperatures below 50°C.

The lack of significant variation in back temperatures for crocodiles selecting materials other than water, in summer specifically, points towards a thermally restrictive pen environment. This suggests the higher temperatures available throughout the on-land portions of the pen in summer, alongside the increased ambient temperature and humidity, may have minimized the crocodile's ability to select the appropriate land-based material for optimal thermoregulation. This interpretation is consistent with the observations of increased numbers of crocodiles occupying the waterbodies in summer and the lower numbers of crocodiles captured in UAV imagery during this season. In contrast, the significant variation in winter crocodile back temperatures between all material types except grass/sand and nests, and grass/sand and concrete, can be explained by the seasonal sparseness of the grassy patches, causing thermal similarity between these material types. Proportionally, land-based pen areas were used more in winter than in summer. This result suggests that summer temperatures may render these areas too hot, resulting in the crocodiles retreating to the water to maintain suitable back/body temperatures.

On average, crocodile back temperature means were higher than positional temperature means. This held true for all dates and times except between approximately 11:30 AM and 14:00 PM on the cool winter's day, where positional temperature means increased above crocodile back means. The strong positive correlations between crocodile temperature and crocodile positional temperature for both seasons is indicative of heat seeking behaviour, and the known dependence of ectotherms on their environmental temperatures. In this case, the crocodiles made use of the various material substrates to seek or avoid warmth by manoeuvring amongst the variable thermal gradients available to them. The range of positional thermal options was relatively narrow in the summer season, starting at around 20°C (compared to the 10°C starting point in winter) and concluding at approximately 50°C (as a posed to 55°C in winter). Notably, the lowest available material/positional temperatures closely corresponded to the lowest back temperatures in both seasons. However, when positional temperatures rose above approximately 20°C in winter and 25°C in summer, the crocodile back temperatures began to level off, few animals reached back temperatures $\geq$40°C. This levelling off might indicate the upper boundary of Nile crocodile thermal comfort. An R^2 value of 0.54 suggests that 54% of the variability in crocodile back temperatures could be explained by the pen material choices in their immediate ambient environments, lending importance to the management of thermal gradients available to crocodiles via the pen materials. The lower R^2 value for summer, when compared to winter, suggests that the crocodiles back temperatures in winter were more predictably modelled from ambient pen temperatures. The range of back temperatures was narrower in summer than in winter but the range of positional temperatures between both seasons was comparable. This finding concurs with the crocodile behaviours studied. In summer the crocodiles were more actively selecting temperatures within the pen by shuttling between land and water, increasing the variability between the observed back and positional temperatures. In winter, longer periods of basking on land were observed, reducing the variability in the observed back and positional temperatures, and likely contributing in the greater R^2 value in the resulting regression equations.

5. Conclusions

A novel, non-disruptive, fast-paced, and highly repeatable method of thermal and behavioural data capture was developed using a relatively affordable UAV platform equipped with a thermal camera (Mavic 2 Enterprise Dual), combined with an IoT system of data loggers. This study assessed the external back temperatures and corresponding positional temperature selections of farmed, breeder sized, Nile crocodiles on a commercial farm in South Africa. It focused on winter versus summer seasonal differences in the thermal regimes available within a breeding pen, and how the captive crocodiles thermally selected appropriate microenvironments within the pen. In particular, the study examined whether warm summer temperatures provided adequate heat avoidance opportunities.

The NSPCAs warnings regarding overheating of farmed crocodiles in South Africa are concerning. The pen assessed in the current study had multiple water bodies and a large land-based area for the crocodiles to move between. During high ambient and pen temperatures in summer, crocodiles sought refuge in water bodies. The results suggest that pen materials (and their thermal properties) are important determiners of crocodile thermal comfort. Farmers should ensure that sufficient basking and heating spaces are available for all crocodiles in winter, and sufficient water/cooling areas for full submersion and shallow lounging are available in summer. Effective shade provision over both land and water areas should be considered during the summer months. Appetites, digestion, growth, and health (Lang, 1987b; Huchzermeyer, 2003; Bothma and Van Rooyen, 2005; Bassetti et al., 2014) are important determinants of crocodilian thermal selection, and require appropriate management.

Future studies utilizing thermal UAVs for assessing environmental thermal regimes, and the thermal responses of crocodiles (or other species) within those environments, might consider recording internal/core T_b and subcutaneous belly/back skin temperatures alongside the surface back temperatures. This could yield valuable information regarding internal body temperatures and a better understanding of the mechanisms and dynamics of crocodile thermoregulation. Expanding the observation periods to include nighttime data and historical data on thermally related mortality and breeding/nesting would enhance our understanding and inform best practises for pen-temperature management and design. From a farming perspective, identifying the areas of the pen that are most thermally "desirable" throughout annual climatic cycles would inform future pen designs in order to enhance optimal thermal conditions in farm settings.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Disclosures

The authors declare that they have no conflicts of interest in this work, the study originates from the first authors PhD (completion by end of 2023) at the University of Pretoria.

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