Effects of stocking density on production and behaviour of farmed grower Nile crocodiles (*Crocodylus niloticus*)

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TABLE OF CONTENTS

	Page
Declaration	5
Acknowledgements	6
Abstract/opsomming	7
Abbreviations	9
Units	10
List of tables	11
List of figures	13
Chapter 1: INTRODUCTION	15
Chautau 2. LITEDATURE REVIEW	17
Chapter 2: LITERATURE REVIEW	17
2.1. Crocodile farming2.1.1 The origin of crocodile farming2.1.2 Current crocodile farming practises	17
2.2. Crocodiles in the wild and in captivity2.2.1 Crocodiles in the wild vs. crocodiles in captivity	18
2.2.2 Crocodile products driving captive crocodile rearing2.3. Growth of crocodiles	19
2.3.1 Captive crocodile growth	
2.3.2 Runtism in commercially farmed crocodiles2.3.3 Measuring crocodile growth	
2.3.4 Manipulation of growth in commercially farmed crocodiles	
2.4. Reproduction in crocodiles	22
2.4.1 Reproductive husbandry on commercial crocodile farms2.4.2 Mating in commercial crocodile farming systems2.4.3 Nesting in commercial crocodile farming systems	
2.4.4 Incubation of eggs on commercial crocodile farms	
2.4.5 Gender classification in commercial crocodile farming systems2.5. Pens and densities	25
2.5.1 Stocking density in current commercial production systems2.5.2 Effect of stocking densities on commercial crocodile production2.5.3 Pen design and density for hatchlings and growers	
2.6. Stress	29
2.6.1 Stress in commercially farmed crocodilians 2.6.2 Assessing stress in crocodilians	
2.7. Housing and Management	30
2.7.1 General housing requirements of farmed crocodilians	50
2.7.2 Pen design	
2.7.3 Pond design and cleanliness	
2.7.4 Temperature regulation in commercial crocodile houses	



	2.8. Digestion, nutrition and feeding	33
	2.8.1 Crocodilian diets	
	2.8.2 Commercial crocodile feeding and nutrition	
	2.8.3 Protein in the commercially farmed crocodilian diet	
	2.8.4 The suitability of plant-based diets in commercial crocodile farming	
	2.8.5 Feeding crocodiles in the grower production stage	
	2.8.6 Feeding practises on commercial crocodile farms	
	2.9. Crocodile farming in South Africa and other developing countries	36
	2.9.1 The viability of commercial crocodile farming in developing countries	30
	2.9.2 Genetic variation in commercially farmed crocodiles	
	•	
	2.9.3 The value of farming crocodiles commercially	20
	2.10. Injuries, diseases and other conditions	39
	2.11. Crocodile skin	39
	2.11.1 Skins: the primary product of commercial crocodile farming	
	2.11.2 Grading of crocodile skins	
	2.12. Crocodile meat	41
	2.12.1 Ideal crocodile killing methods	
	2.12.2 Crocodile meat quality-regulations	
	2.12.3 Crocodile meat characteristics	
	2.13. Crocodile behaviour	42
	2.13.1 Crocodile behaviour in the wild vs. in captivity	
	2.13.2 Forms of communication in crocodiles	
	2.13.3 The importance of behavioural monitoring in crocodile farming	
	2.14. Crocodile welfare	44
Chap	ter 3: MATERIALS AND METHODS	47
	3.1. Animals, housing and climate	47
	3.1.1. Animals and housing	7,
	3.1.2. Processing and handling	
	3.1.3. Daily recordings	
	3.1.4. Climate recordings	
	3.2. Feed intake	50
	3.3. Growth	50
	3.4. Behaviour	50 51
	3.5. Stress	54
	3.6. Skin quality	54
	3.7. Mortalities, illnesses and treatments of crocodiles	56
Chap	ter 4: DATA ANALYSIS	57
6 1.	L. F. DECLUES AND DISCUSSION	
Chap	ter 5: RESULTS AND DISCUSSION	59
	5.1. Climate	59
	5.2. Feed intake	67



5.3. Gr	owth	75
5.4. Be	haviour	88
5.5. Str	ress	107
5.6. Ski	in quality	111
Chapter 6: CON	NCLUSIONS	121
Ch + 7 - CD17	TICAL EVALUATION AND DECOMMENDATIONS	422
Chapter 7: CRII	TICAL EVALUATION AND RECOMMENDATIONS	123
Chapter 8: REF	ERENCES	125
Annexures		129



DECLARATION

I, Devon Marie Veldsman, hereby declare that the content of this dissertation is the result of my own research. Any previous works are referenced in accordance with the requirements of the Faculty of Natural and Agricultural sciences. Apart from the standard guidance of my supervisor and co-supervisors, I make mention of: Mr Roelf Coertze for assistance with the statistical analyses of the study; and Mr Pete Laver, who assisted me in behavioural aspects of the study at the suggestion of my supervisors.

This dissertation is submitted for the degree MSc (Agric) Animal Science: Production Physiology, at the University of Pretoria. The content of this dissertation has not been submitted in any previous works.

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ABSTRACT

The exploitation of crocodilians in the 1950s-1970s resulted in their being listed under the CITES protection appendices. Farming of crocodilians began in South Africa in the 1970s, and has since become an international enterprise, whilst simultaneously playing a role in alleviating the pressure of harvesting from wild populations. A lack of housing standardization for intensive Nile crocodile farming has resulted in commercial farms operating with considerable differences in housing and density. Although this study will not answer the question of a preferred stocking density for every farm trading with the Nile crocodile, the hope is to establish a foundation for standardization in the future.

This study assessed current commercial stocking densities for crocodilians, applied to grower-phase Nile crocodiles at a commercial crocodile farm in Gauteng, South Africa. The pens utilized in the trial were similar in size, shape and design; density was assessed by altering the number of crocodiles assigned to each pen. Three densities (0.43m² per crocodile, 1.24m² per crocodile and 2.60m² per crocodile) were tested in this completely randomised control study, and multiple physiological and behavioural measures were recorded to assess the production and biological responses of crocodiles at these densities. Growth (in the form of morphometric measures), skin quality, stress and behaviours were all monitored over a six-month growth period for 261 Nile crocodiles housed at the abovementioned densities in a commercial crocodile production system.

The present study found that stocking density significantly affected the growth of crocodiles in the trial. The results suggested lower weight gains and condition scores for crocodiles in the lowest density pens compared to those in medium and high-density pens. Skin quality was analysed for every crocodile at the beginning and end of the trial. No during-trial skin analyses were performed for fear of causing the animals unnecessary stress which could yield more antagonistic behaviours, potentially altering skin qualities. The findings indicated no significant differences in pre- and post-trial skin qualities. Possible explanations include adaption to the pens and pen mates, or antagonistic interactions did not yield skin damage to the extent expected. Faecal samples were collected from all pens daily, and a random set of samples selected for analysis. Faecal stress hormone concentrations did not show any significant (P<0.05) differences between the different density groups and appeared to be correlated more to changes in climate over the six-month period. Crocodile behaviour in captivity is not well understood (as in their wild counterparts) but could have many effects and interactions resulting in stress reactions with associated skin damage and reduced growth of some crocodiles in the pens. Time-lapse data were collected for all pens and a random selection of samples used for analysis. The percentages of crocodiles on land or in the water, whether separate from their pen mates or involved in contact and piling behaviours, were studied. Density had significant effects on almost all behaviours observed. This was expected as crocodiles stocked at higher densities had less space to express certain activities, and so behaviours such as piling were seen more regularly.

The findings of this study suggest that the densities assessed did not have the expected effects on all aspects of the young crocodiles' production. There were no significant differences between the examined skin qualities or stress levels of the crocodiles stocked at varying densities in this trial. However, the growth and behavioural recordings differed significantly between the varying densities tested.



OPSOMMING

Die benutting van krokodille sedert 1950s-1970 het veroorsaak dat hulle bygeroeg is onder 'n bylae in die CITES-beskermingswet. Boerdery met krokodille in Suid-Afrika het begin in die 1970s en het sedertien 'n internasionale onderneming geword, veral omdat krokodil boedery in oplossing bied vir die oes van natuurlike populasies. 'n Gebrek aan standardisering van die behuising van intensiewe Nyl krokodil boerdery toon groot verskille in behuising en digtheid op kommersiële plase. Alhoewel hierdie studie nie die vraagstuk oor die huidige behuisingsdigtheid vir elke plaas wat met Nyl krokodille boer kan beantwoord nie, word daar gehoop om riglyne vir standardisering te maak vir die toekoms.

Hierdie studie se doel was om die huidige kommersiële behuisings raaddigtheid vir krokodille te evalueer en spesifiek vir produsente van Nyl krokodille by 'n kommersiële plaas in Gauteng, Suid-Afrika. Die hokke wat gebruik is in die ondersoek, was soortgelyk in grootte, vorm en ontwerp; digtheid is ge-evalueer deur die getal krokodille toegeken per hok, te verander. Drie digthede is getoets in hierdie heeltemaal ewekansige beheerstudie en veelvuldige fisiologiese- en gedragsmaatreëls was aangeteken om die produksie en biologiese reaksies van die krokodille te evalueer by hierdie drie digthede (0.43m² per krokodil, 1.24m² per krokodil en 2.60m² per krokodil). Oor 'n ses-maande groeiperiode, is groei (in die vorm van verskeie morfometriese maatreëls), velkwaliteit, stres en gedrag van tweehonderd-een-en-sestig Nyl krokodille, gehuisves in die voorafbepaalde digthede, in 'n kommersiële krokodil produksie sisteem, gemonitor.

Dit is gevind in die ondersoek, dat behuisings raaddigtheid 'n beduidende invloed op die groei van krokodille gehad het. Die resultate dui op 'n kleiner gewigstoename en swakker kondisie vir krokodille in die laagste digtheid hokke in vergelyking met dié in die medium- en hoë-digtheid hokke. Die velkwaliteit van elke krokodil is ontleed aan die begin en aan die einde van die ondersoek. Gedurende die ondersoek is geen velontleding gedoen nie, omdat gevrees is dat dit die diere onnodig sal stres en antagonistiese gedrag sal ontlok, wat weer moontlike veranderde velkwaliteite kon veroorsaak. Die bevindinge het geen beduidende velkwaliteitsverskille tussen voor en ná die ondersoek uitgewys nie. Moontlike verklarings sluit in aanpassing in die hok en aanpassings met mede-krokodille in die hok, of antagonistiese interaksies het nie soveel skade aan die vel veroorsaak as wat verwag is nie. Fekale monsters is daagliks versamel van alle hokke en die analise in die studie is gedoen op 'n ewekansige wyse met 'n verteenwoordigende porsie van die monsters. Fekale stress hormoon konsentrasies, het ook geen beduidende (P<0.05) verskille tussen die verskillende digtheidsgroepe gewys nie en het eerder gekorreleer met die veranderinge in die klimaat oor die 6 maande periode. Die gedrag van krokodille in aanhouding word nie goed verstaan nie (net soos in die geval van hulle natuurlike eweknieë), maar kan baie potensiële nagevolge hê en interaksies wat stresreaksies tot gevolg het met geassosieerde velskade en verminderde groei van sommige krokodille in die hok. Met verloop van tyd is data versamel van alle hokke en met ewekansigheid is 'n hanteerbare deel van die data gebruik vir analise in die studie. Die persentasie van krokodille op land of in die water, of hulle apart was of in kontak met ander krokodille en of hulle opgestapel was, is bestudeer. Die bevindinge is, dat digtheid 'n beduidende invloed gehad het op omtrent al die gedrag wat bestudeer is. Dit is te verstane, want krokodille wat aangehou word in hoër digthede, sou minder spasie hê om sekere aktiwiteite te doen en het meer opstapeling gedrag getoon.

Die bevindinge van hierdie studie toon, dat die getoetste digthede nie die verwagte effek gehad het op al die aspekte van die jong krokodille se produksie nie. Daar was geen noemenswaardige verskil tussen die vel kwaliteite wat ondersoek is, of die stresvlakke van die krokodille wat aangehou is, teen verskillende digthede nie. Daar was wel 'n groot verskil opgemerk in die groei en gedrag van die verskillende digthede van krokodille wat getoets is.



ABBREVIATIONS

SD stocking density

TBL total body length

SVL snout vent length

BelW belly width

GR growth rate

IR infrared

FGM faecal glucocorticoid metabolites

EIA enzyme immunoassay

FTT failure to thrive syndrome

ERL Endocrine Research Laboratory

CSG Crocodile Specialist Group

SAWS South Africa Weather Service

CITES Convention on International Trade in Endangered Species of Wild Flora and Fauna

FAO Food and Agriculture Organization

SANS South African National Standard

 \overline{x} mean

S.E Standard error

NS non-significant



UNITS

°C degrees Celsius

%RH relative humidity percentage

cm centimetres

m metres

m² metres squared (area measure)

pg picogram

mg milligrams

g grams

kg kilograms

GB gigabytes

\$ dollar



LIST OF TABLES

- 1. Some standard characteristics of the Nile crocodile in the wild, adapted from Intensive wildlife production in southern Africa (Bothma & van Rooyen, 2005).
- 2. Summary of previous studies/documents assessing density effects and the corresponding density recommendations for commercially kept crocodilians.
- 3. (a) Table sourced from Caldwell, 2017. Reported US dollar value of *Alligator mississippiensis* skins (per skin) exported and re-imported by the United States, 2006-2015.
 - (b) Table sourced from Caldwell, 2017. Reported US dollar value of *Caiman crocodilus fuscus* skins (per skin) originating in Colombia and imported by the United States, 2006-2015
 - (c) Table adapted from Caldwell, 2017. Direct, commercial exports of *Crocodylus niloticus* skins from producer countries, 2006-2015.
- 4. Table sourced from Mellor, 2016. Depicts an abbreviated version of the Five Domains Model, for more information refer to the study.
- 5. External (SAWS) and internal (hygrometer) temperature and humidity data (\overline{x} and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa.
- 6. Monthly water and floor temperatures for pens of varying stocking densities (\bar{x} and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa.
- 7. Monthly feed intake per pen and per crocodile for varying stocking densities (\bar{x} and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa.
- 8. Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for low stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.
- 9. Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for medium stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.
- 10. Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for high stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.
- 11. The effects of density on growth traits (\bar{x} and S.E) of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.
- 12. Correlations between growth variables for grower Nile crocodiles stocked at low density at a commercial crocodile farm in South Africa, 2017.
- 13. Correlations between growth variables for grower Nile crocodiles stocked at medium density at a commercial crocodile farm in South Africa, 2017.
- 14. Correlations between growth variables for grower Nile crocodiles stocked at high density at a commercial crocodile farm in South Africa, 2017.
- 15. Cluster means for growth data.
- 16. Frequency table indicating distribution of density groups over clusters for growth data.
- 17. The effect of density on behavioural recordings (\bar{x} and S.E) for grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.
- 18. Correlations for behavioural recordings for grower Nile crocodiles in low stocking density pens at a commercial crocodile farm in South Africa, 2017.
- 19. Correlations for behavioural recordings for grower Nile crocodiles in medium stocking density pens at a commercial crocodile farm in South Africa, 2017.



- 20. Correlations for behavioural recordings for grower Nile crocodiles in high stocking density pens at a commercial crocodile farm in South Africa, 2017.
- 21. Cluster means for behavioural data variables recorded for the water-area of pens.
- 22. Frequency table indicating distribution of density over clusters for water-area recordings in the behavioural data.
- 23. Cluster means for behavioural data variables recorded for the land-area of pens.
- 24. Frequency table indicating distribution of density over clusters for land-area recordings in the behavioural data.
- 25. Correlation table for stress hormone concentrations for grower Nile crocodiles stocked at low, medium, and high densities at a commercial crocodile farm in South Africa, 2017.
- 26. Cluster means for faecal corticosterone concentrations.
- 27. Frequency table indicating distribution of density over clusters for stress data.
- 28. Frequency table showing the effect of stocking density on skin quality of grower Nile crocodiles at a commercial crocodile farm, 2017.
- 29. Frequency table showing the effect of stocking density on skin defects in grower Nile crocodiles at a commercial crocodile farm, 2017.
- 30. Cluster means for skins data.
- 31. Frequency table indicating distribution of density over clusters for skin data.



LIST OF FIGURES

- 3.1 Schematic of trial house, including house dimensions, pen numbers (outer edge of diagram), and the number of crocodiles in each pen. Not to scale.
- 3.2 Schematic of pen layout with lengths and widths of the pen and pond, as well as the pond depth. Not to scale.
- 3.3 Illustration depicting the various morphometric measures used to assess crocodile growth.
- 3.4 Schematic of trial house, with pen numbers (outer edge of diagram) and the camera number (1-8 for each pen in bold next to the cameras identified by small squares), with arrows identifying direction each camera faced.
- 3.5 Sections of a crocodile skin for skin-grading purposes, sourced from: http://www.rojeleather.com/crocodile-skin-grading/
- 5.1.1 Mean monthly maximum, average and minimum ambient in-house temperature, recorded by the hygrometer during the trial period.
- 5.1.2 Mean monthly maximum, average and minimum ambient in-house humidity, recorded by the hygrometer during the trial period.
- 5.1.3 Mean monthly maximum, average, and minimum temperatures for the Hartbeespoort area supplied by SAWS.
- 5.1.4 Mean monthly maximum, average, and minimum humidity for the Hartbeespoort area supplied by SAWS.
- 5.1.5 Mean monthly floor and surface water temperatures in the trial house.
- 5.1.6 Monthly floor temperature for varying density groups in the trial house.
- 5.1.7 Monthly water temperature for varying density groups in the trial house.
- 5.2.1 Mean daily feed intake per crocodile for varying density groups in the trial house.
- 5.3.1 Mean weight measures (pre, post, and difference) for crocodiles housed at varying densities.
- 5.3.2 Pre- and post-trial mean TBL for crocodiles housed at varying densities.
- 5.3.3 Pre- and post-trial mean SVL for crocodiles housed at varying densities.
- 5.3.4 Pre- and post-trial mean BelW for crocodiles housed at varying densities.
- 5.3.5 Mean Fulton's-T (pre, post, and difference) for crocodiles housed at varying densities.
- 5.3.6 Mean Fulton's-S (pre, post, and difference) for crocodiles housed at varying densities.
- 5.3.7 Growth data clusters. coloured and numbered by cluster (cluster 1: black, cluster 2: red)
- 5.3.8 Growth data clusters coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.
- 5.3.9 Growth data clusters. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.
- 5.4.1 Mean percentage of crocodiles viewed in the water per month of trial for varying density pens.
- 5.4.2 Mean percentage of crocodiles viewed on land per month of trial for varying density pens.
- 5.4.3 Mean percentage of crocodiles in the water separate from their pen mates per month of trial for varying density pens.
- 5.4.4 Mean percentage of crocodiles on land separate from their pen mates per month of trial for varying density pens.
- 5.4.5 Mean percentage of crocodiles in the water in contact with their pen mates per month of trial for varying density pens.



- 5.4.6 Mean percentage of crocodiles on land in contact with their pen mates per month of trial for varying density pens.
- 5.4.7 Mean percentage of crocodiles in the water involved in piling with their pen mates per month of trial for varying density pens.
- 5.4.8 Mean percentage of crocodiles on land involved in piling with their pen mates per month of trial for varying density pens.
- 5.4.9 Principal component analysis of the behavioural data.
- 5.4.10 Behavioural data clusters, clustering performed on water-recordings. Coloured and numbered by cluster (cluster 1: black, cluster 2: red, cluster 3: green).
- 5.4.11 Behavioural data clusters, clustering performed on water-recordings. Coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.
- 5.4.12 Behavioural data clusters, clustering performed on water-recordings. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.
- 5.4.13 Behavioural data clusters, clustering performed on land-recordings. Coloured and numbered by cluster (cluster 1: black, cluster 2: red, cluster 3: green).
- 5.4.14 Behavioural data clusters, clustering performed on land-recordings. Coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.
- 5.4.15 Behavioural data clusters, clustering performed on land-recordings. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.
- 5.5.1 Mean faecal corticosterone concentrations per month of trial for varying density groups.
- 5.5.2 Stress data cluster analysis.
- 5.6.1 Principal component analysis of the behavioural data.
- 5.6.2 Skin data clusters. Plotted points have both a shape and a colour; for clarification: points are coloured according to the density group (low density: yellow, medium density: blue, high density: red), shape of the points plotted indicates cluster membership (cluster 1: triangles, cluster 2:circles, cluster 3:plus-signs). The shape of the plotted points is not always easy to discern, and so each cluster group is also encircled on this figure.



1. INTRODUCTION

Crocodile farming is a relatively new industry with multiple areas for improvement and production standardization (Brien *et al.*, 2007). A study in 2000 indicated that crocodile farming in Southern Africa (at the time) was a 25-year-old practise, which began in Zimbabwe (Hoffman *et al.*, 2000). Zimbabwe and South Africa are the leading crocodile-farming countries within Southern Africa, and other participants include: Botswana, Mozambique, Namibia and Zambia (Caldwell, 2017; Beyeler, 2011). The Nile crocodile (*Crocodylus niloticus*), endemic to southern Africa, is one of 15 crocodilian species farmed commercially for their skins (Mpofu *et al.*, 2016; MacGregor, 2006; Bothma & Van Rooyen, 2005; Flint *et al.*, 2000; www.fao.org). Interestingly there are no standardized recommendations regarding space per animal, but rather guidelines that should be considered broad indicators (Isberg *et al.*, 2003; Bothma & Van Rooyen, 2005; Manolis & Webb, 2016). Farming-based practises in South Africa utilise closed systems where no animals are harvested from or returned to the wild. Hatchlings and growers are produced from already farm-owned stock for skin and sometimes meat production. Farming for crocodile skins has allowed the demands of international markets to be met, whilst simultaneously alleviating the pressure on wild populations (Brien *et al.*, 2007; MacGregor, 2006; www.fao.org; <a hr

Captive and farmed crocodiles do not have the same roaming and territory formation opportunities as their wild counterparts for the duration of their lives, they are stocked at higher densities than would occur naturally (Verdade *et al.*, 2006; Isberg *et al.*, 2003). Managing this husbandry aspect is one of the most important when farming crocodiles commercially. There have been multiple studies suggesting negative relationships between stocking density and growth, reproduction, health and skin quality (Brien, 2015; Brien *et al.*, 2007; Bothma & Van Rooyen, 2005; Davis, 2001). Intensive communal pens are the standard in the crocodile farming industry in South Africa. Although standardized guidelines regarding stocking density within the industry are lacking, there are general requirements that need to be met. Some of the requirements are: sufficient space to rest or move, sufficient space to feed and compete for feed, and sufficient space to escape pen mates (Bothma & Van Rooyen, 2005).

Some examples of minimum areas required according to FAO are: 0.1m² per hatchling alligator and 0.3m² per 1-3-year-old alligator. According to SANS (SANS 631:2009 Edition 1), the national standards for Nile crocodiles in captivity in South Africa are as follows: crocodiles older than one year (approximately 750-2000mm in length) require 0.75-2m² per animal, whereas adult crocodiles require a minimum of 10m² each. In terms of stocking densities, the following studies have made their own recommendations based on their findings: Elsey² et al. (1990) worked with juvenile alligators and recommended ≥1.8m²/alligator; Poletta et al. (2008) worked with hatchling broad snouted caiman and recommended 0.1m²/caiman; Davis (2001) worked with hatchling to one year old crocodilians and recommended 0.3m²/crocodile of the weight 4-5kg, and 0.6m²/crocodile at 12-26 months of age or weighing 9kg. Some recommended densities according to Crocodile Farmers Association of Zimbabwe (CFAZ): Codes of Practise (CFAZ, 2012) for Crocodylus niloticus in Zimbabwe are as follows: no more than 15 individuals/m² for hatchling crocodiles (greater than 0.07m² area per individual), 2-4 individuals/m² for 1-1.5 metres long raising stock (between 0.25 and 0.5m² area per individual), and 1-2 individuals/m² for 1.5-2 metres long rearing stock (between 0.5 and 1m² area per individual). Hatchlings in this case are categorized as being between 0 and 9-11 months of age, rearing stock refers to yearlings (one year of age) and grower stock thereafter (CFAZ, 2012).

Pens are a substantial capital investment and should be designed for the optimization of growth of young crocodiles (Bothma & Van Rooyen, 2005; Isberg et al., 2003). An absence of



standardization in crocodile housing has led to multiple studies, as seen above, utilizing varying stocking densities (SD) with varying results in various crocodilian species; including: saltwater crocodiles, American alligators and the broad snouted caiman (Poletta *et al.*, 2008; Davis, 2001; Elsey² *et al.*, 1990; www.fao.org; SABS, 2009). The lack of information surrounding a commercial standard SD for intensively farmed Nile crocodiles has led to significant SD variations from farm to farm, with many crocodilian farmers labouring under the impression that crocodiles can simply be grouped into whatever area is available, thereafter they are expected to produce and reproduce efficiently. The issues to be addressed through a study of SD's are: a lack of knowledge surrounding a standardized SD for captive Nile crocodile rearing; the lack of quantification regarding welfare concerns of stress levels in farmed Nile crocodiles at varying SD's; and the potential effects of inappropriate housing and SD on the skin quality and growth of farmed early-grower Nile crocodiles. All parameters to be recorded (growth, stress levels, skin quality, and behavioural variations) in the current study were suspected to be correlated with stocking density. The aim of the study was therefore to compare current commercial stocking densities employed in intensively farmed early grower Nile crocodiles on a commercial crocodile farm in Gauteng, South Africa. The hypotheses were as follows:

H_o: Grower crocodiles housed at lower stocking densities would endure less antagonistic interactions, due to the greater potential for avoidance manoeuvres. If this were true, such crocodiles should have lower faecal corticosterone concentrations, and potentially greater skin qualities and growth rates.

H_{A:} Grower crocodiles housed at greater stocking densities would endure more antagonistic interactions and competition among pen mates. This could potentially lower their growth rates, and lead to more extensive skin damage, along with higher faecal corticosterone concentrations.



2. LITERATURE REVIEW

2.1 Crocodile farming

2.1.1 The origin of crocodile farming

Crocodilian farming and ranching, for both commercial and conservation purposes, has received much attention in recent years (Manolis & Webb, 2016; Tosun, 2013; MacGregor, 2006; Elsey et al., 1990). The exploitation of natural populations of multiple crocodilian species in the 1950s - 1970s led to the implementation of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) protection acts in 1975 (Manolis & Webb, 2016; Mpofu et al., 2016; Tosun, 2013; Wallace & Leslie, 2008; Brien et al., 2007; MacGregor, 2006; Bothma & Van Rooyen, 2005; Flint et al., 2000; Hoffman et al., 2000; www.iucncsg.org [1]; www.fao.org). Crocodiles were caught and killed mainly for their skins for sale in international markets (Manolis & Webb, 2016; MacGregor, 2006; www.fao.org). Commercial crocodile farming contributes to the conservation of a widely exploited species, all crocodile species currently fall within appendices I and II of CITES regulations (Manolis & Webb, 2016; Beyeler, 2011). Animals listed under appendix-I are threatened by extinction and are not to be utilized unless produced in a captive-breeding setting. Those under appendix-II are not currently threatened but could become so in the future if their utilization is not controlled (Beyeler, 2011; MacGregor, 2006; www.iucncsg.org [1]). The Nile crocodile specifically is listed under both appendices (population dependent), based on their numbers in the wild they are not considered truly endangered (Blessing et al., 2014; Beyeler, 2011; MacGregor, 2006; Flint et al., 2000), but are still conservation dependent (Bothma & Van Rooyen, 2005). Illegal activities of wildlife trade or poaching are still occurring regardless of the CITES regulations. There are at least 30 countries involved in CITESapproved export of crocodilians, and all such skins are tagged for authenticity (Ityavyar et al., 2011; MacGregor, 2006). The rate of utilization in recent years has resulted in captive rearing of crocodilians for conservation, and conscious sustainability of their wild counterparts. Crocodile farming began in South Africa in the 1970s (Mpofu et al., 2016; Bothma & Van Rooyen, 2005; Flint et al., 2000; Elsey et al., 1990; www.iucncsg.org [1]).

2.1.2 Current crocodile farming practises

There are two broad types of captive crocodile keeping, namely farming and ranching. Ranching originated in Zimbabwe in 1965 and involves the harvest of crocodilian eggs or hatchlings from wild populations, the crocodiles are hatched and/or reared on farm until slaughter. Ranching practices can include incentives for conservation of the wild species through breeding, tourism or education initiatives (Mpofu *et al.*, 2016; Tosun, 2013; Beyeler, 2011; Wallace & Leslie, 2008; Brien *et al.*, 2007; MacGregor, 2006; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002; www.iucncsg.org [1]; www.iucncsg.org [1]; www.iucncsg.org [1]; www.fao.org). Some ranching systems release of a portion of animals from egg collections once they have reached a size where they are no longer in threat of predation in the wild (www.fao.org). Ranching for production till slaughter has the unavoidable drawbacks of inconsistency between harvests, and variation in quality between harvests (Beyeler, 2011).

Farming-based practises are also known as "captive breeding" and utilise closed systems, where no animals are harvested from or returned to the wild. Stocks are produced from the already farm-owned stock for skin and meat production, this is the case for farming crocodilians in South Africa (Ganswindt *et al.*, 2014; Brien *et al.*, 2007; MacGregor, 2006; www.iucncsg.org [1]; www.fao.org). Captive breeding practices can also utilize a tourism-based initiative to supplement their income and encourage local education and job-creations; however, these systems are generally more production than conservation based (Wallace & Leslie, 2008; Brien *et al.*, 2007; Flint *et al.*, 2000; www.iucncsg.org [1]; www.iucncsg.org



indirectly to the conservation of crocodilian species via alleviation of the demand for wild crocodile products (Brien *et al.*, 2007; MacGregor, 2006; www.iucncsg.org [1]). Farming operations often face difficulties in their setup and sustainability, especially in developing countries. Inappropriate husbandry practices regarding housing, feeding and hygiene yield issues such as: disease, mass mortality, and therefore poor marketing stability (Brien *et al.*, 2007). The reality of egg production in captivity as the most cost-efficient method for crocodile farming became apparent in the 1970s. Although the crocodile industry is newly emerged, it is making progress moving from extensive outdoor practices to intensively managed environmentally-controlled housing systems (Bothma & Van Rooyen, 2005; Davis, 2001). The shift towards captive breeding has had an important effect on skin quality; with fewer injuries the quality is greater than that of wild crocodiles. The resulting increase in first grade skins has led to the shrinking of the market for second and third grade skins (MacGregor, 2006). The aim of any wildlife farming enterprise should be the satisfaction of local and international demand without compromising the stock left in the wild. This must be achieved without compromising the product quality or animals' welfare for the duration of captivity (Ityavyar *et al.*, 2011).

2.2 Crocodiles in the wild and in captivity

2.2.1 Crocodiles in the wild vs. crocodiles in captivity

Of the living reptile species, crocodiles are the largest. Crocodilians can live in various habitats of both salt and freshwater; with some species surviving in both habitat types, such as the saltwater crocodile (Crocodylus porosus) (Ityavyar et al., 2011). Human activities have altered wild crocodile habitats and numbers in recent years; it is believed that breeding in captivity is a viable method for their replenishment (Ityavyar et al., 2011). There are 24 species of crocodile recognised throughout the world; only 15 of these species are traded in commercially for their skins. The Nile crocodile (Crocodylus niloticus) is the only one of these species' endemic to southern Africa (Mpofu et al., 2016; MacGregor, 2006; Bothma & Van Rooyen, 2005; Flint et al., 2000; www.fao.org; www.iucncsg.org [2]). There is a perception of the crocodile farming industry in southern Africa as "individualistic", with no standard production techniques for the farmers to base their systems on (Bothma & Van Rooyen, 2005). A study in the year 2000 indicated crocodile farming in South Africa (at the time) was a 25-yearold practise, which began in Zimbabwe when farming from wild-harvested eggs was licensed in the early 1960s (Hoffman et al., 2000). Lake Kariba in Zimbabwe was one of the pioneering African sites of intensive Nile crocodile production in 1965 (Beyeler, 2011; Bothma & Van Rooyen, 2005). Crocodiles were harvested at an early age (eggs or hatchlings) from the wild and raised in captivity under intensive rearing conditions (Mpofu et al., 2015; Bothma & Van Rooyen, 2005). This shift towards intensive rearing was primarily due to the depletion in numbers attributable to overzealous harvestings in previous years; as well as finding that these wild-sourced animals did not all thrive in captivity after having been harvested from the wild (Bothma & Van Rooyen, 2005). Nile crocodile farming was originally extensive (eggs sourced from the wild), but there has been a recent shift towards intensive production (eggs are sourced from already owned breeding stock) (Bothma & Van Rooyen, 2005).

A reality faced by crocodiles raised in captivity is an environment of extreme social challenges and reduced space compared to their wild counterparts, enduring stress challenges which reduce production and reproduction, and therefore survivorship (Brien, 2015; Brien² et al., 2014; Tosun, 2013; Huchzermeyer, 2002). Adaption capability of the crocodiles, and the ability to tolerate these captive-stresses, determines the success of production (Brien, 2015; Brien² et al., 2014). The following welfare requirements must be met when a wild species is farmed in captivity: the supply of appropriate and balanced diets, fresh water at all times, sufficient space for natural behaviours, protection from predation, disease preventative measures and timely treatments (Tosun, 2013). Crocodiles have a



natural fear of humans from the time they hatch, in captive breeding situations the larger animals over-come their fear (Brien, 2015; Bothma & Van Rooyen, 2005). This does present safety issues during feeding and nest-protecting stages. All workers engaging with these animals must be sufficiently educated in interpretation of crocodilian behaviours and follow a strict system of rules for their own safety (Brien, 2015; Bothma & Van Rooyen, 2005).

2.2.2 Crocodile products driving captive crocodile rearing

Skins have long been the primary product of the commercial crocodile farming industry, with crocodile meat becoming popular in recent years as a secondary source of income to supplement the increasing production costs associated with stricter market requirements (MacGregor, 2006; Hoffman et al., 2000; www.fao.org). The majority of South African produced crocodile meat is exported and sold for human consumption. Alternatively, any excess meat or off-cuts can be fed back into the production system as crocodiles are naturally cannibalistic in the wild (Tosun, 2013; Hoffman et al., 2000; www.fao.org). Zimbabwe takes advantage of the excitement surrounding such an unusual meat by selling to surrounding game park restaurants for tourist consumption (Hoffman et al., 2000). Some other uses of crocodile products include medicinal uses, religious uses, parts for decorative purposes, and finally oil and claws (Wallace & Leslie, 2008; www.iucncsg.org [1]). According to the IUCN-SSC Crocodile Specialist Group (CSG), current legal trade in crocodile skins involves 1.5 million skins annually from approximately 30 countries. International trade in skins involves the following species primarily: Crocodylus niloticus (Nile crocodile), Crocodylus siamensis (Siamese crocodile), Crocodylus porosus (Saltwater crocodile) and the American alligator (Alligator mississippiensis). (Mpofu et al., 2015; MacGregor, 2006; www.iucncsg.org [1]). For more information regarding other minority species refer to Caldwell (2017).

2.3 Growth of crocodiles

2.3.1 Captive crocodile growth

As in any farming situation, production in terms of growth is dependent on an animal's genetics, and living-environment. There seems to be a general lack of interest among crocodile farmers with regards to genetics, apart from the knowledge that renewing stock periodically is beneficial in avoiding genetic disturbances and fixations (Blessing et al., 2014; Bothma & Van Rooyen, 2005; Davis, 2001; Flint et al., 2000). The management of the crocodile's environment is the current factor determining the growth of farmed crocodiles; the farmer and the technologies available to him/her will determine the success of the enterprise. Crocodiles in ranching or farming situations grow better than their wild counterparts; where temperature is controlled, food is supplied, and predation is completely avoided (Brien² et al., 2014; www.fao.org). Table 1 depicts some standard characteristics of the Nile crocodile in the wild, the values recorded in the aforementioned table would differ for captive or farmed crocodilians. Growth rates of various crocodilians in captivity have been shown to be higher than the tabulated values and will vary from farm to farm depending on stock and management thereof (Bothma & van Rooyen, 2005; www.fao.org). Farmed crocodiles can reach sexual maturity given proper management and nutrition, it should be noted that farmed crocodilians can reach sexual maturity earlier then their wild counterparts given proper management (Brien et al., 2014; www.fao.org). There are factors of production that must be considered and controlled to ensure optimal growth rates, such as: confinement at greater densities than would be encountered in the wild, social hierarchies, competition and dominance within groupings of animals, and finally human disturbances. A study by Groffen et al. (2013) assessing Philippine crocodiles in their first year of life noted stress in crocodile farming is unavoidable due to inappropriate temperatures, stocking



densities, handling, inadequate nutrition, human disturbances and poor management. Farmers should aim to minimize such stresses through proper management, thereby conserving immunocompetency and growth rates, and minimizing hatchling mortality (Isberg & Shilton, 2013; Poletta et al., 2008; Elsey² et al., 1990). The growth measures used in the study were: total body length, snout-vent length, tail length, neck and tail circumferences and body weight (Groffen et al., 2013). Stress is not to be underestimated in crocodile farming practices, with the causes varying from poor housing to poor feeding regimes and/or poorly trained staff members (Isberg & Shilton, 2013; Beyeler, 2011; Poletta et al., 2008; Elsey² et al., 1990). These studies concur that stress levels and growth rates go hand in hand in commercial crocodilian rearing situations. The effects of such chronic stress impacts growth negatively, for example: Elsey² et al. (1990) studied growth rates (GR) and plasma corticosterone concentrations (the primary glucocorticoid stress hormone of crocodilians) in juvenile alligators stocked at varying densities. The findings concluded that an inappropriately high stocking density led to reduced growth rates, owing to more dominance interactions and therefore growth suppression in the smaller individuals, as a result of severe stress (Elsey² et al., 1990). A 2014 study by Shilton et al. (2014) concurs with these findings, stating that "Corticosterone levels are negatively correlated with GR in both saltwater crocodiles and alligators with regard to runtism". Raised Corticosterone levels are also known to be associated with immuno-depression; subsequent disease epidemics can reduce the growth of an entire farms' crocodiles (Shilton et al., 2014).

Table 1 Some standard characteristics of the Nile crocodile in the wild, adapted from Intensive wildlife production in southern Africa (Bothma & van Rooyen, 2005).

Growth rate (length)	300mm/year (optimal conditions!)
Mean length at maturity	3m females and 4m males
Mean mass at maturity	150kg female and 400kg male
Feeding spectrum	Mainly fish, mammals and insects
Preferential hunting time	Night
Mean number of eggs per clutch	45 (30-90)
Incubation period	90 days
Nest temperature	30-32 degrees
Egg mass	100-120g
Age at sexual maturity	10-12 years
Age at first mating	10-12 years female & 15-20 years male
Time between successive clutches	12 months
Life expectancy	70 years
Females per male in wild	1.6
Recommended females per male in captivity	8
Survival rate in wild	2%
Territoriality	Generally only the males

2.3.2 Runtism in commercially farmed crocodiles

As mentioned previously, captive survival rates are greater than those of wild crocodile populations and this is highly management dependent (Brien¹ et al., 2014; www.fao.org). A growth abnormality seen in all captive crocodile species (on all commercial farms) is runting, also known as the failure to thrive syndrome (FTT). This syndrome is the primary cause of death in captive hatchlings (Brien, 2015; Brien¹ et al., 2014). FTT has been reported at rates of 10-20%, and in severe cases in up to 50% of hatchlings born in captivity (Brien, 2015). Afflicted individuals can be identified within the first 24 days of life by exceptionally poor growth rates. FTT affected crocodiles are smaller in size than



their clutch mates, with obvious poor muscling, severely reduced fat deposits in the body and tail, lower albumin levels, higher corticosterone levels, and early-onset osteoporosis (Brien¹ et al., 2014; Shilton et al., 2014). Runts are managed on commercial farms by removing them from the presence of their larger siblings and grouping them separately to allow for more equal feeding opportunities (Shilton et al., 2014). Runtism, even when managed effectively, can never be fully reversed (Brien, 2015). Afflicted animals represent a greater feeding and maintenance cost than their healthy counterparts and have a lowering effect on potential incomes (Shilton et al., 2014). The cause of runtism is poorly understood, the following factors have been suggested as being involved in the extent of this issue on farm: genetics, maternal condition at time of mating and laying, incubation conditions, chronic stress, poor housing and temperature maintenance, inappropriate stocking density, and poorly formulated diets (Brien¹ et al., 2014; Shilton et al., 2014).

Hatchling size and growth rates differ between species, populations, and siblings (Brien¹ et al., 2014). Individual variation is always present and significant variations have been recorded between clutch mates, raised on the same farm, under identical rearing conditions (Brien, 2015; Shilton et al., 2014; www.fao.org). Regular sorting into separate size-determined groups (away from their larger siblings) and a high protein diet are required if runts are to be fed up to a marketable size with any hopes of gaining a profit. It has been shown that hatchling growth and survival is not affected by initial size. In fact, smaller hatchlings grow faster in the post-hatch period, yet larger hatchlings exhibited better initial growth and survival rates (Brien, 2015; Brien¹ et al., 2014). The findings of a particular study showed that saltwater crocodile hatchlings able to gain 4-7g within the first 24 days of life had a greater survival potential, and less chance of enduring FTT afflictions (Brien¹ et al., 2014).

2.3.3 Measuring crocodile growth

Crocodile growth is measured in various ways, each has its own advantages or disadvantages. The easiest way to weigh crocodiles, when they are still of a size where they can be handled, is suspension from a box or sack over a spring balance (www.fao.org). The two main length measures are total length (TBL) and snout vent length (SVL). Total length is advantageous as the animal can be quickly captured and measured whilst on its belly. The disadvantage of this measure is the occasional loss of the ends of tails due to fighting and dominance behaviours (www.fao.org). Snout vent length as a measurement is advantageous in that there are lower risks of incorrect measures as might be encountered when evaluating total length; however, this method requires the crocodile be flipped onto its back, this is more stressful for the animals. Whenever handling crocodiles for measurements such as these, whether full grown or not, the snout should be secured shut and the eyes covered for the safety of both the handlers and crocodiles (www.fao.org). Belly width has been used frequently when measuring crocodilian growth, however care must be taken with this measure as the crocodiles have to be turned onto their backs which can be stressful. It has also been suggested that breathing can sometimes affect this measure when it is applied to live crocodiles. This is suggestive of belly width not being an ideal growth measure, however it is still of importance for international sale of skins (Blessing et al., 2014; Bothma and van Rooyen, 2003; Isberg et al., 2003; www.fao.org). Neck and tail circumferences have also been used in previous studies assessing crocodilian growth (Groffen et al., 2013).

2.3.4 Manipulation of growth in commercially farmed crocodiles

In commercially farmed domestic species the improvement of growth through the manipulation of hormones is widely practised. Growth promoting implants for example have been used in species such as cattle and sheep for many years. A study by Finger *et al.* (2016) discussed the potential for applying this in crocodile farming. The study compared oestrogen (not related to growth



in the specific study) and testosterone levels in slow versus faster growing Saltwater crocodile hatchlings. The larger crocodiles had lower testosterone levels than their smaller counterparts. Interestingly, the slower growing juveniles had greater testosterone levels; according to Finger *et al.* (2016) this contrasts with findings reported for wild American alligators and captive Nile crocodiles (Lance *et al.*, 2015; Rooney *et al.*, 2004, Morpurgo *et al.*, 1992). Testosterone levels were highest immediately before the breeding season began in juvenile and adult Saltwater crocodiles, with the lowest testosterone levels found in the coolest months. If the manipulation of testosterone for example could be controlled, there could be potential to improve on-farm growth. Furthermore, the lessening of aggression between captive crocodiles in commercial farming systems could be achieved; thereby reducing stress reactions/interactions which have been found to negatively affect both growth and reproduction (Finger *et al.*, 2016).

2.4 Reproduction in crocodiles

2.4.1 Reproductive husbandry on commercial crocodile farms

Husbandry practises for commercially farmed crocodilians encompass breeding, incubation of eggs, and hatchling management. Crocodiles reach sexual maturity between 4-15 years of age depending on breed, general management, and quality of feed supplied. If faster growth can be encouraged at a young age, sexual maturity can be reached at a younger age. As age and maturity progress, the number of eggs and fertility of embryos will improve (Lance et al., 2015; Magnino et al., 2009; Brien et al., 2007; www.fao.org). Successful captive breeding relies on multiple factors including the size of the male, male to female ratios, and optimal stocking rates (Brien et al., 2007; Verdade et al., 2006). Sex ratios of approximately eight females to one male are recommended, ideally in their own breeding pen to maximise fertility rates and prevent conflict between males, but this is not always economically viable (Brien et al., 2007; Bothma & Van Rooyen, 2005; www.fao.org). Male crocodiles should be larger than the females, but of a similar size with other breeding males to ensure dominance interactions do not prevent certain males from mating (Brien et al., 2007; Verdade et al., 2006; Bothma & Van Rooyen, 2005). Stocking densities in breeding camps can be maximised via alterations in pool and enclosure shapes, more bends and barriers within a pond allow greater stocking densities (Brien et al., 2007; Verdade et al., 2006). Crocodiles in captivity tend to exhibit poor reproduction as a result of the stress, injuries and social disruptions involved with poor pen designs (Brien et al., 2007; Verdade et al., 2006). Verdade et al. (2006) studied diurnal space used by broad snouted caimans. Often territoriality (extent of which is species-specific) is restricted to mating seasons; female crocodiles specifically are defensive of their clutches if housed in mating groups with a single male. The largest and most aggressive animals dominate the mating and nesting activities. Housing caimans of a similar size together can aid in the formation of stable reproductive groups, along with the arrangement of isolated (as far as possible) nesting shelters for the avoidance of antagonistic reproductive behaviours (Brien et al., 2007; Verdade et al., 2006).

South African crocodile farmers originally sourced their breeding stock from neighbouring countries (i.e.: Zimbabwe, Botswana and Mozambique); this is no longer an option, and producers now buy from one another in the hopes of keeping their on-farm genetics viable and gaining new animals which will produce well (Tosun, 2013; Bothma & Van Rooyen, 2005). Adults and juveniles are sold to this purpose; adults are generally preferred as they are immediately useful in the system. In future when making such purchases, juveniles of known-producers may be purchased and raised to the producer's standards to become a viable mating female between 10 and 12 years of age. Keeping records of breeding and hatchability successes can give farmers an idea of how well their stocks are producing (Tosun, 2013; Bothma & Van Rooyen, 2005; www.fao.org).



2.4.2 Mating in commercial crocodile farming systems

Mating is generally seasonal in wild crocodilian species and will depend on climate and environmental conditions of the habitat in which the animals are found, commercially kept crocodilians mimic this seasonal breeding (Davis et al., 2001; www.fao.org). Grouping of crocodiles is an important factor to consider for successful captive breeding. In the wild male Nile crocodiles become territorial during the mating season - this holds true in farmed populations too and therefore sufficient space per breeding male is an important requirement. Territorial males will chase other competing males from the females and snap their jaws or roar loudly (Tosun, 2013; Davis et al., 2001; www.iucncsg.org [3]). Mating itself occurs in the water (preferably 2m deep for full submersion); a single pair can mate multiple times, occasionally resurfacing for air. Repetitive matings are necessary as each mating only fertilizes a portion of the eggs; in the wild females seek out multiple males yielding clutches of varying paternal origin (Tosun, 2013; Bothma & Van Rooyen, 2005; www.iucncsg.org [3]). Captive crocodiles have fewer territoriality options on commercial farms, simplifying paternal traceability to an extent. Even in captive breeding instances, it can never be assumed that only one male in a breeding pen fertilized an entire clutch (Bothma & Van Rooyen, 2005; Davis et al., 2001).

2.4.3 Nesting in commercial crocodile farming systems

Nesting behaviours usually begin 2-3 weeks after mating activities, crocodilian species vary in their nesting behaviours (Tosun, 2013; www.iucncsg.org [3]). Some species prefer to dig a hole to lay eggs in (such as the Nile crocodile) whilst others are mound-builders, where the eggs are laid and then covered with natural materials in a mound. The female Nile crocodile digs her 0.4-0.5m deep nest with her back legs, lays between 30 and 90 eggs, and then covers her nest (Tosun, 2013; Bothma & Van Rooyen, 2005; www.iucncsg.org [3]; www.iucncsg.org [3]; www.iucncsg.org [3]; www.fao.org). There are also behavioural differences in nest protection, with some species or individuals defending their nests aggressively, and others leaving the nests almost unguarded. The wild female Nile crocodile (and those on commercial farms) guards her nest throughout the incubation period of about 90 days. The length of incubation is temperature dependent, with some nests hatching as soon as 11 weeks after laying, and others as late as 14 weeks after laying (Tosun, 2013; Bothma & Van Rooyen, 2005; www.iucncsg.org [3]; www.fao.org). An incubation period of approximately 76 days is preferred for Nile crocodile eggs artificially incubated on farms (Prof J.G. Myburgh personal communication 2018).

Nile crocodiles lay one clutch per female per year in the wild, this is similarly mimicked in captive Nile crocodiles. Egg laying periods differ in varying regions of Africa, in most of South Africa eggs are laid in September and October (Bothma & Van Rooyen, 2005; www.fao.org). In captive breeding situations the provision of sufficient nesting area influences nesting success and therefore reproductive success; as well as reducing fighting over nesting sites. These nest-sites should be easy to access and far from deep water for worker safety during collections (Brien et al., 2007). Stress caused by both nest defence and abandonment can be detrimental to the reproductive capabilities of commercial breeding animals. Nile crocodile females are nest guarders and must be kept at bay by one handler, whilst another collects the clutch contents (Bothma & Van Rooyen, 2005). Recordings of collections should be concise, with records such as: the number of nests collected from, the number of eggs per nest, egg weights, egg measurements, the number of deformed or damaged eggs (these eggs are removed and not allowed to proceed to incubation), and finally the number of eggs that actually hatch (Bothma & Van Rooyen, 2005, www.fao.org).



2.4.4 Incubation of eggs on commercial crocodile farms

Incubation involves the collection of eggs as soon as possible after they are laid, removing excess sand from the eggshell, marking of position laid (the eggs should be placed in the incubator in the same orientation in which they were collected from the nest site) and placing the eggs in an incubator (Brien et al., 2007; Bothma & Van Rooyen, 2005; www.fao.org). Temperatures within incubators determine embryo development, fertility, and the sex of the hatchlings. The incubation period generally lasts 65 (artificial incubators) to 90 (wild nests) days at a steady 32 (can vary between 31 and 33) degrees Celsius (°C), and at a minimum humidity of 90 %RH (Tosun, 2013; Magnino et al., 2009; Bothma & Van Rooyen, 2005; www.iucncsg.org [3], www.fao.org). Generally temperatures of less than 30°C yield more females in a clutch, whereas temperatures above 31.5 to 32°C yield more males in a clutch (Bothma & Van Rooyen, 2005; www.iucncsg.org [3]; www.fao.org). In alligators: a steady nest temperature of 32°C yields an 80:20 female to male clutch, and 34°C or higher will yield exclusively male hatchlings. These nest temperatures yield similar results in the Nile crocodile, and notably: a higher proportion of males is preferred in commercial systems as males grow faster within the first year of life, minimising their time in the farming system and therefore optimizing profitability (www.fao.org). Developmental consequences related to failure to maintain optimum incubator temperatures have been recorded for various crocodilian species. For example, embryo deformities increase in occurrence when temperatures above 34°C are allowed during incubation; whereas temperatures below 28°C have yielded arrested development, smaller hatchlings and greater occurrences of runting (Bothma & Van Rooyen, 2005; www.fao.org). Electronic digital thermometers monitor temperatures in the incubator when eggs are packed or collected, allowing timely rectification of unwanted temperature shifts.

Humidity plays a role in moisture maintenance in the incubator, which is important for embryo health (Bothma & Van Rooyen, 2005; www.fao.org). Vermiculate is the preferred insulating material for artificial nesting in incubators to date. Insulation supplies the eggs with both the moisture and aeration required, whilst also insulating the eggs from swift temperature changes. In the wild hatchlings cannot escape their nest alone and must signal the adult female crocodile to dig them out by chirping (Tosun, 2013; Bothma & Van Rooyen, 2005; www.fao.org). In artificial incubation the eggs are not covered deeply, temperatures are maintained at optimum and the hatchlings do not need to escape a deep pit of sand and organic materials. In the wild the chirping of one hatchling is known to stimulate its clutch-mates into hatching; this is so in artificial incubators as well. For this reason, human-induced noises and disturbances should be minimized during hatching (Tosun, 2013; Bothma & Van Rooyen, 2005; www.fao.org). Some factors reducing the success of incubation in captive breeding situations are as follows: stress, obese breeding females, deficiencies in the diet, aggressive protection-behaviours of nests placed too close together, and poor handling of the fragile eggs between nest and incubator (Bothma & Van Rooyen, 2005; www.fao.org).

2.4.5 Gender classification in commercial crocodile farming systems

Gender classification in crocodiles is important for breeding procedures on farms and for ethological research with wild crocodilians (Lance et al., 2009; Ziegler & Olbert, 2007; Tucker & Limpus, 1997). Crocodiles can be manually sexed via the palpation and/or protrusion of the male penis from within the cloaca (usually accomplished using a finger), which can thereafter be compared to the smaller female clitoris (Ziegler & Olbert, 2007; Tucker & Limpus, 1997). Sexing can be complicated in juvenile (difficulty distinguishing male from female genitalia) and mature (in terms of handling) crocodiles due to their size (Ziegler & Olbert, 2007; Bothma & Van Rooyen, 2005; www.fao.org). Another consideration is that of the morphological variations between species and individuals. Expertise is required in procedures of sexing young crocodiles as the organs are only vaguely different



to the untrained eye at an early age (Ziegler & Olbert, 2007; Bothma & Van Rooyen, 2005; www.fao.org). As crocodiles grow the male penis grows significantly larger and is easier identified. It is notable that males grow larger over time and tend to have broader tail bases; these characteristics can be helpful when sexing older crocodilians but should not be relied upon for sexing juveniles (Ziegler & Olbert, 2007). Previous studies have utilised ultrasound to diagnose follicular development in female crocodilians (Lance et al., 2009; Tucker & Limpus, 1997), it would not be a stretch of the imagination to consider using ultrasonography for sexing farmed crocodilians if the resources for this were readily available.

2.5 Pens and densities

2.5.1 Stocking density in current commercial production systems

When reviewing stocking density, one should consider whether the information pertains to hatchlings, growers (also called rearing stock) or breeders.

Communal pens have been the standard for a number of years in the crocodile farming industry (Isberg *et al.*, 2003; Bothma & Van Rooyen, 2005). In captivity, crocodiles are stocked at greater densities, and numerous studies in crocodilians have found multiple negative effects between stocking density and growth, reproduction, health and skin quality (Brien, 2015; Bothma & Van Rooyen, 2005; Davis, 2001). Although there is no scientific based evidence for a specific surface area (land and water) per animal; sufficient space to move, feed, and escape pen mates is a general requirement (Isberg *et al.*, 2003; Bothma & Van Rooyen, 2005). Pens are a substantial financial cost and should be designed for the optimization of production and reproduction activities (Isberg *et al.*, 2003). Stocking density is one of the most important aspects of raising crocodiles in captivity; in the wild crocodiles have space to move around and form territories (Beyeler, 2011; Verdade *et al.*, 2006; Isberg *et al.*, 2003).

Refer to Table 2 for recommended densities proposed as guidelines for crocodilian farming, note this table is composed of various studies or sites, with varying crocodilian species included. Hatchlings in this case are categorised as being between 0 and 9-11 months of age, rearing stock refers to yearlings (one year of age), and grower stock would be over one year of age (CFAZ, 2012). A study referencing the 2012 CFAZ document suggests that these recommendations are but broad indicators, and assessments should be made periodically so that adjustments can be made based on the health, growth and skin quality of stock (Manolis & Webb, 2016).

When considering breeder crocodiles: reproduction is significantly affected by poor housing and pen designs; with minimal egg fertility and increased embryonic mortality encountered in poorly housed females. Few farms achieve first year survival rates over 95% due to housing and management inaccuracies (Isberg *et al.*, 2003).



Table 2 Summary of previous studies/documents assessing density effects and the corresponding density recommendations for commercially kept crocodilians

Species	Growth phase	Density recommendation	Reference
Saltwater	Hatchling	0.07- 0.1m ² /crocodile	Manolis & Webb, 2016
crocodile			(referencing CFAZ, 2012)
	Raising stock (1 m	0.25- 0.5m ² /crocodile	u
	in length)		
	Raising stock (2 m	1-2 m ² /crocodile	u u
	in length)		
Nile crocodile	Hatchling	>0.07m ² /crocodile	u
	Raising stock (1-	0.25- 0.5 m ² /crocodile	u u
	1.5m in length)		
	Raising stock (1.5-	0.5- 1m ² /crocodile	u u
	2m in length)		
American	Raising stock	>0.09 m ² /alligator	"
alligator	(<0.6m in length)		
	Raising stock (0.6-	0.27 m ² /alligator	"
	1.2m in length)		
	Raising stock	0.36 m²/alligator	u
	(>1.2- 1.35m in		
	length)		
	Raising stock	0.45 m ² /alligator	u
	(>1.35- 1.5m in		
	length)	21.0	
	Raising stock	Add 0.09 m ² /alligator for	u
	(>1.5m in length)	every 0.15m above 1.5m	
		total length	
American	Hatchling	0.1m ² /alligator (minimum)	www.fao.org
alligator	(4.2)	>0.2 · 2/- III · · · · ·	"
A.11 111	Grower (1-3 year)	≥0.3m²/alligator	2442 524 222 5 111
Nile crocodile	Grower (>1 year)	0.75- 2m²/crocodile	SANS 631:2009 Edition 1
	Adult	≥10m²/crocodile	
American	Juvenile	≥1.8m²/alligator	Elsey et al., 1990
alligator		2.1	
Broad snouted	Hatchling	0.1m ² /caiman	Poletta et al., 2008
caiman		24.11	
American	Hatchling (<1	0.3m ² /alligator	Davis, 2001
alligator	year)	0.0.27 111	и
American	Juvenile (1-2	0.6m ² /alligator	"
alligator	years)		

2.5.2 Effect of stocking densities on commercial crocodile production

Poletta *et al.* (2008) conducted a study on growth under varying stocking densities in commercially farmed broad snouted caiman hatchlings. Crowding in such situations yielded poor growth and an increase in the number of injuries to the skin due to dominance and fighting (Poletta *et al.*, 2008). Body mass gain and tail length growth were increasingly retarded as the stocking density increased. Faster growing caimans are preferred for their likely survival and shortened time on the



farm, therefore reducing the costs of production (Poletta *et al.*, 2008). Brien (2015) ran a trial analysing growth rates of hatchling saltwater crocodiles (*Crocodylus porosus*) housed at different densities; raised under the same conditions in terms of other housing factors, environment and feed. The hatchlings, all the same age, were randomly selected from five clutches and grouped at the following densities: 0.3, 0.15, 0.08, and 0.05m²/hatchling (Brien, 2015). Growth was measured between 4-25 days of age using the variable: body mass. The findings were as follows: the largest hatchlings had lower growth rates than the smaller hatchlings; the density group with the best overall growth rate was the group housed at the second lowest stocking density of 0.15m²/hatchling; the group with the poorest growth rate was the group housed at the highest stocking density of 0.05m²/hatchling. The proposed reason for the high density stocked groups having poorer growth rates overall was the higher rate of agonistic dominance interactions in these groups (Brien, 2015). Some hatchlings grew faster and used their size as an advantage in gaining dominance over the smaller pen-mates, preventing these smaller crocodiles from eating and therefore growing as efficiently. The lower growth rates overall at higher densities could be due to an increase in activity, these youngsters not only had less space to move but engaged in more dominance behaviours (Brien, 2015).

Where grower crocodiles are concerned, pens of inadequate dimensions can lead to reduced activity, such animals are prone to obesity and the related negative effects of cardiac disease and reduced fertility. Crocodiles housed in close-quarters tend to fight more, and the subsequent reduced skin quality and increased stress levels lead to production and reproductive disturbances. Bullying and fighting can be reduced by ensuring adequate area provision, and by the planned housing of individuals of a similar size together to avoid dominance interactions (Brien *et al.*, 2007; www.fao.org).

Breeder crocodiles should be allowed to reach their full size, breeder space requirements are significant and most often these animals are kept in large groups (Brien et al., 2007). There should be multiple females per male, with the males of similar size to ensure equal mating opportunities (Ityavyar et al., 2011; Brien et al., 2007; www.fao.org). Sufficient space will also reduce the chances of fighting, bullying, and dominance interactions among both males and females during mating periods (Brien et al., 2007; www.fao.org). Elsey¹ et al. (1990) studied the relationship between stocking density and nesting success, taking blood samples from both wild and captive adult American Alligators for the monitoring of plasma Corticosterone (the primary reptilian stress hormone). The study aimed to reveal the economic practicality of current captive crocodilian raising systems (Elsey¹ et al., 1990). Findings from previous studies indicate that growth rates were greater in captive Alligators, but the eggs produced had low fertility and hatchability in comparison to those found in wild populations. There are various potential reasons for this distinction, including: farmed Alligators are encouraged to grow fast at a young age therefore speeding up sexual maturity, poorly planned stocking densities, and nutritional deficiencies (Elsey¹ et al., 1990). The findings of the aforementioned study were as follows: male alligators in both captive and wild groups were found to have higher plasma Corticosterone levels; captive alligators at the greatest stocking densities had the lowest reproductive success and highest corticosterone levels (Elsey¹ et al., 1990).

2.5.3 Pen design and density for hatchlings and growers

From as early as a few days after hatching young crocodiles should be placed into groups of similar sized youngsters, this will reduce early food competition and therefore stunting of smaller individuals at such a young age. Every two months or so the animals should be re-grouped according to size, the first year is the most important in terms of growth and so these regroupings are highly necessary (Brien, 2015; Bothma & Van Rooyen, 2005).

Rearing pens differ from farm to farm, but generally young crocodiles are kept in closely monitored groups during rearing phases (Bothma & Van Rooyen, 2005). Overstocking in



raising/grower pens causes increases in skin damage, owing to the fact the young animals are continuously climbing over one another, and sitting or lying on top of each other (Bothma & Van Rooyen, 2005). The solution to date to this issue is the elongation of rearing pens; the Zimbabwean pen designs use 20m x 13m pens with two long ponds of 16m x 3m each. This design allows sufficient dry area for the animals to rest without clumping together excessively, and also reduces stress by giving greater water area for the young animals to hide and cool off in (Bothma & Van Rooyen, 2005). The ponds for the above design are maximum 1m deep, allowing the young crocodiles to stand in the water with just their eyes and nostrils exposed, or to fully submerge and swim short distances. The slope should be approximately a 30-degree angle, or less to allow ease of access to, and exit from, the water (Bothma & Van Rooyen, 2005).

With the shift from extensive to intensive farming of crocodiles in recent years, single pens have come of interest to producers (Isberg & Shilton, 2013; Webb et al., 2013; MacGregor, 2006; Bothma & Van Rooyen, 2005). Currently single pens are used for the final grow out or "finishing" phases, to allow healing of skin blemishes caused by fights and aggression in group-rearing situations (Isberg & Shilton, 2013; Webb et al., 2013). There have been studies into the viability of this type of housing at earlier production stages, which could potentially minimize skin blemishes from earlier ages, and reduce Corticosterone levels (Isberg & Shilton, 2013; Webb et al., 2013). There have also been many clashes of opinion as to whether this would be acceptable in terms of welfare of the crocodiles (Webb et al., 2013; Huchzermeyer, 2003). Young crocodiles in the wild group together until about 3-6 months of age, after which the mother sends them away by shaking them in her mouth causing the young to fear cannibalism by larger crocodiles. Once these animals reach sexual maturity and are large enough that they do not feel as threatened, they come back together (Unpublished report, Huchzermeyer). Farmed crocodiles do not have the same experiences as their wild counterparts; instead they adapt to social hierarchies from a young age and endure them up until slaughter. Occasional intolerances still occur in farming situations, and fighting can cause damage to the skin (Webb et al., 2013; Huchzermeyer, 2003). Saltwater crocodiles for example are known for their aggression even in captive farming situations (Brien, 2015). Young crocodiles are more socially inclined and grow well in groups where they can band together to feel safe. Once they become large enough for dominance reactions however, captive Saltwater crocodiles tend to fight and have lower growth and survival rates than that of other farmed crocodilians such as the Nile crocodile, or Alligator mississippiensis (Brien, 2015).

Webb et al. (2013) compared communal and single pens in terms of the potential advantages and disadvantages of each, this study concluded that single pens are a viable production type. Communal pens have the advantages of being inexpensive to install and having lower feeding and cleaning costs than that of single pens. The disadvantages of communal pens were as follows: management of individuals is impossible, hierarchies and social conflicts are unavoidable, individual growth rates vary dramatically due to the dominance interactions that inevitably occur, and finally the periodic rearrangements into similar-sized groups can be disruptive and yield safety issues for both staff and animals. Single pens have the disadvantages of being expensive to install and maintain, with pen-design variances confusing the farmers as to what the specifications of the ideal single pen would be. The advantages are however extensive, and include: minimization of social intolerances and stress, allows the healing of any blemishes or injuries, management on an individual level is possible, skin quality is improved (>70% first grade skins produced), and finally there have been no documented adverse health effects of housing in single pens (Webb et al., 2013). A study comparing crocodiles on two farms, some in single and some in communal pens, concluded no significant differences in corticosterone levels in crocodiles housed communally or in single pens (Isberg & Shilton, 2013). The question being asked by crocodile producers is if single pens could solve the aggressive interaction issues encountered in communally housed animals, as well as the potential for these pens to improve



the quality of skins produced (Huchzermeyer, 2003), without compromising the basic welfare requirements of commercially farmed animals.

2.6 Stress

2.6.1 Stress in commercially farmed crocodilians

Stress can be broadly defined as any factor that displaces homeostasis. Stress is important to a livestock producer due to its influence on animal health, production and reproduction (Moleon *et al.*, 2018; Sheriff *et al.*, 2011; Huchzermeyer, 2003; Stott, 1981). Any stimulus inducing a stress response in an organism is known as a stressor. Stress is unavoidable in crocodile farming situations, and can be the result of social stressors, management and housing stressors, and environmental stressors. It is therefore essential to monitor and, if possible, correct for potential stressors and their effects (Ganswindt, 2014; Elsey² *et al.*, 1990; Stott, 1981). Chronic stress can occur in crocodiles housed at inappropriate stocking densities, where fleeing from one another is complicated by a lack of space. Stress on a continual basis can yield multiple negative effects on an animal's production, reproduction and immune system (Ganswindt *et al.*, 2014; Isberg & Shilton, 2013; Huchzermeyer, 2003; Elsey¹ *et al.*, 1990; Elsey² *et al.*, 1990; Stott, 1981).

A study involving wild-harvested juvenile broad snouted caimans tested multiple stressors and the effects on stress and immunological reactions in these animals. The findings of the study showed that caimans housed at higher temperatures, and fed regularly and sufficiently: grew better, had lower stress responses, and higher immune tolerance (Moleon *et al.*, 2018). Another study which was conducted with finishing farmed saltwater crocodiles (*Crocodylus porosus*) showed chronically stressed animals having raised glucocorticoid stress hormones; leading to reduced health, resistance, growth, survival and affinity for wound healing (Isberg & Shilton, 2013).

2.6.2 Assessing stress in crocodilians

Hormone analyses (sampled from blood, hair, urine, faeces, or saliva) are widely used for monitoring reproductive activity, metabolic activity, and stress responses in many species. Sampling activities can induce stress due to the need for capture, immobilization, handling and the methods of sampling (Ganswindt et al., 2014; Ganswindt, 2013; Sheriff et al., 2011; Brien et al., 2007; Elsey¹ et al., 1990). Non-invasive techniques have been gaining popularity as they avoid the potential alteration of stress levels induced by excessive handling (Ganswindt et al., 2014; Ganswindt, 2013). This is particularly useful when working with stress prone species, and in farming situations where animals have regular human interaction and handling (Ganswindt et al., 2014; Ganswindt, 2013; Brien et al., 2007). Recent developments in faecal steroid metabolite analyses in various species have allowed the reduction of handling-based stresses; which were previously necessary when attaining blood or plasma samples for hormone analyses. Some noteworthy advantages of faecal steroid analyses are that it is non-invasive, there is the possibility for long-term sample collections (making this information applicable in conjunction with other parameters in a study), and finally there is potential for animal husbandry applications (via furthering comprehension of endocrine physiology of farmed animals) within farming systems (Schwarzenberger, 2007). There are also some factors potentially affecting the viability of faecal steroid analyses, including: steroid metabolism and excretion, sample storage, diet, gender, and variations according to season (Sheriff et al., 2011; Schwarzenberger, 2007). Assay validation of faecal steroid analysis is essential due to species-specific differences (Ganswindt et al., 2014; Ganswindt, 2013; Sheriff et al., 2011; Schwarzenberger, 2007).

Ganswindt *et al.* (2014) assessed the viability of faecal glucocorticoid metabolite (FGM) analysis for the non-invasive monitoring of adrenocortical functioning of captive Nile crocodiles.



Stress, and potentially chronic stress, is faced in most crocodile farming systems in South Africa. The disturbance of homeostasis induces increased glucocorticoid secretions that if endured at high levels over long periods of time can negatively affect health, production and reproduction (Ganswindt *et al.*, 2014). In recent years it has become necessary to develop non-invasive sampling methods, specifically for wild and easily stressed species, such as the crocodile. The FGM approach allows minimal disturbance and handling of the animals, and collections can be easily incorporated into a farming schedule, i.e.: sample collections coinciding with cleaning or feeding schedules (Ganswindt *et al.*, 2014). The study was not without complications due to hormone-circulation lags and infrequent defecations (both of which can be attributed to stress); as well as unstable temperatures or nutrition, and variation between individual crocodiles. Plasma and faecal samples were analysed for comparison, the findings showed that elevated corticosterone concentrations inhibited growth rates. This study verified the use of faecal glucocorticoid metabolite analyses for stress assessment for the Nile crocodile (Ganswindt *et al.*, 2014).

2.7 Housing and management

2.7.1 General housing requirements of farmed crocodilians

Crocodiles are large predatory reptiles, and farming of the species does not mean that they are domesticated (Brien *et al.*, 2007; www.fao.org). Crocodiles are stress prone animals therefore inappropriate management, housing, feeding, and care of these animals' leads to chronic stress reactions. The negative effects of this are extensive and, if not managed, lead to significant production and reproductive losses (Brien *et al.*, 2007). Stressed crocodiles do not grow efficiently, have poorer survival rates, become disease prone, endure reproductive failures, and have inferior skin quality (Brien *et al.*, 2007; Verdade *et al.*, 2006; www.fao.org). Pen design, as discussed above, is only one aspect of managing the farming environment. There are multiple housing related factors involved in adequately housing these large reptiles, including: water quality, feeding practices, temperature regulation, shelter availability, training of on-farm personnel, and hygiene maintenance (Brien *et al.*, 2007; www.fao.org).

Location is the first vital factor in successful captive crocodile rearing, environments with climates as close to those which wild crocodiles inhabit are ideal (Bothma & Van Rooyen, 2005, www.fao.org). Warm summers and dry cold winter areas have seen better production than areas of minimal radiation and cold/wet winters (Bothma & Van Rooyen, 2005). Stress due to unnecessary disturbance; especially in young, human-fearing crocodiles; leads to reduced growth and production. Similarly, large adults should not be disturbed unnecessarily. Proper training of personnel is essential for both the animals and the keepers' safety in the case of both young and full-grown crocodiles (Brien et al., 2007; Bothma & Van Rooyen, 2005). Feed management will be discussed later, but on that note, keepers and caretakers should be knowledgeable when feeding crocodiles of feeding behaviours and social hierarchies. A 2011 study of Nile crocodile captive management (Ityavyar et al., 2011) found that on-farm deaths were primarily due to inadequate feeding, and feed competition between crocodiles (Ityavyar et al., 2011; www.fao.org). Multiple studies concur that sufficient feeding space per animal and spreading the feed out over the area of the pen reduces feed-related fighting and dominance of the larger animals over their smaller counterparts (Blessing et al., 2014; Ityavyar et al., 2011; Isberg, 2007; Bothma & Van Rooyen, 2005, www.fao.org).

2.7.2 Pen design

Floors and walls of crocodile pens are generally smooth concrete; however, plastics have been recommended for minimal skin damage (Shilton *et al.*, 2014). Concrete flooring is used frequently



when housing crocodilians; in warmer climates this material conserves heat, assisting crocodilian appetite stimulation and subsequent growth (Blessing et al., 2014; Brien et al., 2007; Huchzermeyer, 2003). An important aspect of smooth concrete flooring; although it is easily cleaned and yields minimal skin damage compared to many other flooring types; in colder environments there is potential for heat loss via conduction from the crocodiles bodies (Shilton et al., 2014; Bothma & Van Rooyen, 2005; www.fao.org). In such cases it has been recommended that insulation be provided under the concrete flooring of pens, or copper piping run through the concrete floor to heat up water bodies at night, this is especially important in hatchlings (Bothma & Van Rooyen, 2005, www.fao.org). Walls in rearing pens should be a metre tall with smooth polyurethane sealing, and of a neutral colour such as a light grey to mimic a natural environment (Bothma & Van Rooyen, 2005). Safety for both animals and handlers/feeders is a primary concern in the crocodile farming industry. It is recommended that walls be not only of a sufficient height but also curved inward, especially in breeding pens, so that animals cannot climb out. A sufficient number of gates, far from the water, with easy dual-sided locking mechanisms are also recommended (Brien et al., 2007; www.fao.org). Barriers or hiding boards placed within large pens allow both visual and physical separation of crocodiles, reducing stress and therefore ensuring proper growth (Groffen et al., 2013; Brien et al., 2007). Brien² et al. (2014) studied the effect of water depth and the inclusion of barriers in the pens of hatchling saltwater crocodiles on growth and agonistic behaviours. Their findings indicate that shallower water with visual barriers reduced antagonistic interactions when compared with shallow water with no barriers (Brien² et al., 2014). The nature of interactions in deeper water with barriers was more peaceful than in deep water without barriers, probably due to the fact that the animals had sufficient space to turn and swim away from one another unhindered. Although the results were interesting, no statistically significant effects on growth rate were found in any treatment group (Brien² et al., 2014).

2.7.3 Pond design and cleanliness

It is generally recommended for water-bodies/ponds to cover approximately 50-70% of an enclosure. The water should not be too deep; crocodiles should be able to stand comfortably with tails resting on the bottom of the pond (30-50cm deep for juveniles, and at least 1m for adults), and a gradual ascent between water and land allows the animals to easily exit the water ("hauling out") (Shilton et al., 2014; Brien et al., 2007; Bothma & Van Rooyen, 2005; www.fao.org). Crocodiles unable to exit the water without slipping and sliding could cause damage to the skin of their bellies and feet (Bothma & Van Rooyen, 2005). An angled cement extension of 1m around the pool allows easier haul out and reduces food and faecal debris entering the pool (Brien et al., 2007). Fresh water is ideal, especially for young crocodiles in the hatchling and rearing stages. Water is often drawn from nearby rivers or dams where crocodiles do not live naturally, this is an important distinction as there is a high risk for disease contamination if water is sourced from areas accommodating wild crocodilians (Brien et al., 2007).

Water temperature is an essential growth-determining factor, this is important in farming situations where the air temperatures cannot be precisely controlled. In such instances maintaining the water temperatures at optimums allows the crocodiles seek out warmth when needed (Brien, 2015; Shilton *et al.*, 2014; Isberg, 2007; Davis, 2001). Another important requirement for ponds is that they are spacious enough for all crocodiles to submerge simultaneously (Brien *et al.*, 2007; Bothma & Van Rooyen, 2005). Water cleanliness is a major hygiene factor for both crocodile and handler, and the clarity of the water enhances handler safety (Brien *et al.*, 2007, Bothma & Van Rooyen, 2005). There are differing opinions on the ideal shape of pools, with corners and turns being preferred so the crocodiles can separate themselves if they feel the need, thereby reducing stress and aggression.



Natural ponds are advised against due to their cleaning requirements and propensity for hygiene, disease and treatment related issues (Brien *et al.*, 2007). A 2015 study (Mpofu *et al.*, 2015) found that natural ponds (also referred to as "earth ponds") resulted in smaller skins after processing; whereas cement ponds had a greater percentage of first grade skins when compared to earth ponds. Cement ponds are recommended for easy cleaning and unchallenging footing for the crocodiles, especially in juvenile and sub-adult housed groups (Mpofu *et al.*, 2015).

Cleaning and pond-drainage are other water-related housing factors considered important for ideal crocodilian management. Farming and ranching facilities will differ in their frequency of water-drainage depending on the environment, number of crocodiles housed, water-restrictions, and available resources (Brien *et al.*, 2007). Outlets should ideally be located at the bottom of the pond with valves located outside of the pens; this allows maximal drainage and cleaning away of faeces and excess food, without disrupting the animals (Tosun, 2013; Brien *et al.*, 2007; Bothma & Van Rooyen, 2005). Cleaning frequency should be as often as possible, even daily if this can be managed. Cleaning at times such as feeding can be beneficial in minimizing the frequency of human-related disruptions (Brien *et al.*, 2007; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002).

Daily removal of uneaten food is necessary to maintain hygiene and ensure minimal bacterial levels within the ponds. The occasional scrub out of ponds with disinfectants is also recommended, the ponds are to be thoroughly rinsed down before refilling and allowing crocodiles back into the area (Brien *et al.*, 2007). During cleaning and feeding times it is important for the staff to avoid disturbing the crocodiles, especially younger animals due to their keen fear of humans (www.fao.org).

2.7.4 Temperature regulation in commercial crocodile houses

Crocodiles are poikilothermic, meaning they have an inability to thermoregulate by physiological means; this is where the term 'cold-blooded' originated (Tosun, 2013; Hoffman *et al.*, 2000; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002; www.iucncsg.org [4]; www.fao.org). The crocodile's external environment is the determinant of its temperature (Bothma & Van Rooyen, 2005). The ideal temperature range is approximately 24-32°C, this is maintained through exercises such as basking, mouth-gaping and moving between sunny and shaded areas (Brien, 2015; Shilton *et al.*, 2014; Tosun, 2013; Bothma & Van Rooyen, 2005; www.iucncsg.org [4]; www.fao.org). The mouth-gaping action mentioned above as a temperature-balancing mechanism, has also been determined to be a behavioural response indicating a warning to leave the crocodile alone (www.iucncsg.org [4]). Temperature maintenance is important for both health and growth of crocodiles; fluctuations could lead to reduced growth, survival and disease resistance (Brien, 2015; Brien *et al.*, 2007). Indoor temperatures and water temperature maintenance is essential; technological advancements in the form of heating elements have been useful in perfecting the control of these factors (Brien, 2015; Brien *et al.*, 2007).

Optimal growth rates are achieved at approximately 31°C; digestion and therefore growth is reduced when temperatures fall below 29°C. A study of growth at varying temperatures in saltwater crocodile hatchlings (Brien, 2015) found that hatchlings provided constant warm temperatures through both day and night had better growth than hatchlings supplied heat only during the day. With recent technological advances, constant temperature regulations are attainable and essential to maximizing early growth in crocodiles (Brien, 2015). Temperatures must be maintained for optimal digestion, crocodiles will even seek out heat post-feeding; this is called thermophily (Bothma & Van Rooyen, 2005). If there are unregulated temperature drops, young crocodiles will have a greater affinity for fat deposition as opposed to growth.

Sufficient heat is an important aspect but so is sufficient cooling and shade options should be provided (Brien, 2015; Brien et al., 2007; Davis, 2001; www.iucncsg.org [4]). Vegetation and shade



netting are both viable forms of cover when crocodiles need to lower their body temperatures (Tosun, 2013; www.fao.org). If temperatures fall below an approximate 15°C, Nile crocodiles show disinterest in feeding. Temperatures as low as 7°C (or lower) can cause reduced movement capabilities and crocodiles have drowned in cases where temperatures were not properly controlled (www.fao.org).

Maintenance of body temperatures is more difficult for a small crocodile; whereas the larger animals are able to store some heat during the day to last into the night; small animals require stricter temperature control. Roofs of enclosures that slope northwards are better (in the Southern hemisphere) for capturing maximal sunlight during the day (Bothma & Van Rooyen, 2005). The material of the roof will also impact the amount of heat retained; aluminium, glass and fibreglass have all been used as roofing materials. Insulation within the roof materials is also a recommendation. With all the heat-retaining technology, extractor fans will be needed to induce the required air movement during the day so as not to over-heat the crocodiles (Bothma & Van Rooyen, 2005; www.fao.org). All doors into the building should be airtight, and nearby washing facilities are recommended (Bothma & Van Rooyen, 2005).

2.8 Digestion, nutrition and feeding

2.8.1 Crocodilian diets

Wild crocodilian diets are indiscriminate, opportunistic and tend to change as they mature. Young animals feed near the shore on small crustaceans and insects, with maturity crocodilian diets expand to include fish and varying sizes of mammals as well as these smaller prey items (Blessing et al., 2014; Tosun, 2013; Beyeler, 2011; Wallace & Leslie, 2008; Isberg, 2007; Bothma & Van Rooyen, 2005; www.iucncsg.org [5]; www.fao.org). There has been a misconception in the past of crocodiles preferring rotting meat, and even "storing" meat to allow it to rot before eating it (Tosun, 2013; Bothma & Van Rooyen, 2005). The reason behind this was the visualization of crocodiles leaving large carcasses for a few days in the wild before eating them. However, this is explained by the thick hides of larger mammals softening a few days after death, once the hide is more malleable the crocodiles can consume it with less effort, thereby conserving energy (Tosun, 2013). From what has been recorded in crocodile farming situations, these animals prefer fresh meat (Bothma & Van Rooyen, 2005; www.fao.org). Fresh meat is also recommended for health reasons, to minimize potential bacterial infections. Refrozen meats should preferably not be fed to commercially farmed crocodilians, and some meats require cooking before being fed (Brien et al., 2007; www.fao.org). Meats that have been thawed, or that were not frozen when fresh are susceptible to bacterial contamination. With chicken forming the primary feed protein for commercially farmed crocodilians in Africa, Salmonella is a concern (Isberg, 2007; Huchzermeyer, 2002; www.fao.org). Refreezing thawed meat would be doubly dangerous in this case. Farmers should constantly re-assess the feed requirements of their stock to avoid thawing of more feed than is needed, and therefore avoiding the prospect of post-thaw re-freezing. Although cooking some meats before feeding is possible to avoid certain bacterial contaminations, fresh meat is the preferred choice. This has led to one of the chief conundrums faced by the industry to date: the availability of fresh meat (Brien et al., 2007; Bothma & Van Rooyen, 2005; www.fao.org).

2.8.2 Commercial crocodile feeding and nutrition

Feeding and nutrition can account for 45-60% of commercial crocodilian production operating costs; this varies between operations depending on available protein sources and environmental differences (Blessing *et al.*, 2014; Beyeler, 2011; Isberg *et al.*, 2003; Pinheiro & Lavorenti, 2001).



Crocodiles require high protein diets usually composed of low-fat red meats or chicken; along with supplementary amino acids, minerals and vitamins often presented in the form of premixes (Brien, 2015; Blessing *et al.*, 2014; Beyeler, 2011, Brien *et al.*, 2007; Isberg, 2007; www.fao.org). Crocodile stress levels, skin quality, bone quality and immune capability are dependent on a balanced diet with well formulated premixes (Blessing *et al.*, 2014; Brien *et al.*, 2007). Calcium is particularly important, and dietary levels should be monitored and adjusted according to the crocodile's requirements (Brien, 2015; Shilton *et al.*, 2014; Brien *et al.*, 2007; www.fao.org).

Farmers in Africa have relied on chicken meat as their main protein source, with supplementary meats from stables/stockyards/supermarkets when available or if required. Often only one type of meat is fed, vitamin and mineral premixes are essential in such cases. Another option is the purchase of fresh fish as an extra source of vitamins and minerals if the crocodiles eat it (Bothma & Van Rooyen, 2005; www.fao.org). Variation of proteins within the initial diets fed to young crocodiles (hatchlings) can be the determinants of survival rates and fitness (Brien, 2015; Brien et al., 2007; www.fao.org). On farms based in areas with chicken as a primary feed source, issues with Salmonella have been encountered, and there are strict feeding rules in place to minimize this (Isberg, 2007; Huchzermeyer, 2002).

2.8.3 Protein in the commercially farmed crocodilian diet

Differences in feed protein availability and affordability (which vary with location) are the primary determinants of costs of feeding (Brien, 2015; Isberg, 2007; www.fao.org). Feed conversion efficiency should be optimized so as to minimize feed costs (Blessing et al., 2014; Isberg et al., 2003). There have been multiple studies delving into the ideal types and inclusion percentages of protein that should be fed to commercially farmed crocodilians for their optimal growth and production (Blessing et al., 2014; Beyeler, 2011; Isberg, 2007).

Blessing *et al.* (2014) conducted a study using varying dietary protein levels (50%, 55%, and 60%) in hatchling Nile crocodiles, and compared the growth rates of these animals. The hatchlings were fed *ad lib*, daily, for 3 months; with weekly random selections of crocodiles from each pen for measurements of growth (measures used: belly width and total body length). The findings concluded the 60% protein diet-fed hatchlings had the greatest belly widths, the animals' lengths did not differ significantly between the 55% protein and 60% protein fed hatchlings. Therefore the 60% protein diet was recommended (Blessing *et al.*, 2014).

Ideally the future farmers and producers involved with crocodile farming should prioritize perfecting crocodile diets. Poor nutrition combined with the stress of captive farming may lead to reduced growth, fertility, and immunity; as well as increased incidences of bone and teeth disorders, and poorer skin quality (Brien *et al.*, 2007).

2.8.4 The suitability of plant-based diets in commercial crocodile farming

The development of an artificial diet would be beneficial for crocodile farming systems worldwide in terms of availability of ingredients, as well as affordability (Isberg, 2007; Bothma & Van Rooyen, 2005; Davis, 2001). Although multiple studies have been conducted in Australia for the saltwater crocodile; ranging from formulated feed pastes to pellets of varying carbohydrate/fat /protein levels, and when to initiate the feeding of such diets; no "ideal" standardised diet has been created or approved (Isberg, 2007). Extensive research into the diet of the American alligator and Nile crocodile has yielded a pelleted artificial diet (Beyeler, 2011; Isberg, 2007; Bothma & Van Rooyen, 2005; Davis, 2001). The advantages of artificial feeds include reduced capital requirements and maintenance costs (more readily available protein sources, no need for refrigeration, and extended storage capabilities), as well as reduced labour costs (cleaning requirements) and potential for



contamination (Isberg, 2007; Bothma & Van Rooyen, 2005; Davis, 2001). With crocodile farms in South Africa feeding chicken as the primary protein source for crocodiles, an artificial alternative could benefit both crocodiles and humans as it could reduce the competition for this protein between humans and commercially kept crocodiles (Isberg, 2007; Huchzermeyer, 2002; www.fao.org). Crocodilians are known for their fussy eating habits, this fact complicates the formulation of an artificial feed due to the need for perfection of certain feed factors like texture, odour and taste (Beyeler, 2011; Bothma & Van Rooyen, 2005). These factors have been the major contributors to the failure of a plant-based protein feed source to date (Beyeler, 2011; Isberg, 2007; Davis, 2001). A study assessing soybean meal as a protein source in the saltwater crocodile showed a reduction of 25% in early growth rates. Digestibility coefficients were also measured in this study, and both the digestibility of protein and energy was reduced with the soybean diet (Isberg, 2007). It is fairly apparent that the advantages that artificial-based diets would afford producers in terms of affordability would come at a major production cost. A study by Beyeler (2011) confirms this for the Nile crocodile specifically: the 5-6-month-old Nile crocodiles from this study showed a feeding preference for animal-based proteins, as well as a greater efficiency if digestion when such proteins were maximised in the young crocodile diets.

2.8.5 Feeding crocodiles in the grower production stage

The first year of life is the most important in terms of growth and feeding during this period should ideally be on a daily basis and approximately 15-20% of live body weight. Only once crocodiles have reached sub-adult size (only require an intake of 10% of their body weight) should feed frequency be reduced (Brien, 2015; Blessing *et al.*, 2014; Brien *et al.*, 2007). These are only guidelines of course; individual requirements will vary according to age, production stage, stress factors, and quality of nutrition (Blessing *et al.*, 2014; Brien *et al.*, 2007; www.fao.org).

Hatchlings in captivity can be offered food from the day of hatch; this minimizes the chances of stunting (due to early food competition) or runting (Bothma & Van Rooyen, 2005; www.fao.org). There are producers that delay feeding for the first week or two when yolks are still visible after hatch, this ensures that the egg yolks are fully utilized. Technically this should not be necessary if incubation was performed properly, in which case the majority if the yolk would have been utilized for in-egg growth pre-hatch (Bothma & Van Rooyen, 2005; www.fao.org). Keeping hatchlings dry, warm (34°C ideal) and protected from flies and other insects should speed up yolk absorption and prevent infections of the yolk or umbilical cord (www.fao.org). Once feeding begins, an initial feeding of 20g/hatchling/day should be sufficient, once the young crocodiles are eating more routinely the feed amounts can be adjusted weekly according to feed residues and increases in the size and appetites of the young animals (Bothma & Van Rooyen, 2005; www.fao.org). It is recommended that food be chopped or minced for juveniles to reduce fighting and messing during feeding (Bothma & Van Rooyen, 2005; www.fao.org). Brien (2015) recommended chopping the feed into bite sized pieces, making it easier for the youngsters to grab and hold onto the food, thereby reducing the amount of feed wasted or thrown into the water during feeding scuffles.

Feed intake and growth are positively correlated, with underfeeding leading to reduced growth, and overfeeding leading to obesity and the associated health issues (as well as poor egg development) (Blessing *et al.*, 2014; Tosun, 2013; Brien *et al.*, 2007; Davis, 2001). Growth rates decrease as crocodiles increase in age and are especially slow as the animals approach maturity (www.fao.org). A study of feeding frequency of farmed crocodiles in differing size-classes found that crocodiles fed more frequently had greater feed conversion efficiency (FCE); as well as finding that smaller animals grew more efficiently in both weight and length than the crocodiles in the larger-classed group (Davis 2001). It was suggested that the lower FCE in the larger crocodiles could have



been due to fighting induced stresses, as these animals determined their social hierarchy. The study also noted that when feeding occurred less often during the week the feeding interactions were more aggressive, the stress resulting from such interactions could be detrimental to FCEs (Davis, 2001). Ityavyar *et al.* (2011) noted a positive relationship between feed intake and reproductive rates of the Nile crocodile, yet another reason to ensure good feed intakes and preferably high-quality feeds.

2.8.6 Feeding practises on commercial crocodile farms

Feeding on-farm is recommended towards the end of the day, when external temperatures are dropping and there is less chance of food wastage due to the feed baking in the sun throughout the day (Bothma & Van Rooyen, 2005; www.fao.org). Feeding needs to follow a calm routine so as not to cause unnecessary stress and the crocodiles racing around the enclosures, causing damage to themselves and their pen mates (Bothma & Van Rooyen, 2005).

Body temperature regulation determines a crocodile's rate of metabolism and digestion is impaired if an animals' temperature drops. If the temperature cannot eventually be raised food will rot inside the stomach, resultantly the body is poisoned (Bothma & Van Rooyen, 2005; www.fao.org). Intake is greater during the warmer months of the year (Blessing et al., 2014; Brien et al., 2007; www.fao.org). Crocodiles have the ability to sense weather fluctuations, possibly by detecting atmospheric pressure changes, and often will stop eating before a cold front (Blessing et al., 2014; Bothma & Van Rooyen, 2005; www.fao.org). The issue with extended periods of cold weather is the ability of crocodiles to survive a few months without any food; they slowly wither away and cannot be made to eat if they are unwilling (www.fao.org).

2.9 Crocodile farming in South Africa and other developing countries

2.9.1 The viability of commercial crocodile farming in developing countries

Crocodile farming is a relatively new industry with multiple areas for potential improvement and production standardization. There are production difficulties as with many animal husbandry practises, these are compounded in developing countries where some simple requirements are unavailable or cannot reliably be met (Brien *et al.*, 2007). Some such issues faced include a lack of electricity, clean water availability, land area requirements, animal feed requirements, and varied or available breeding stock (Brien *et al.*, 2007). The reality of crocodile farming is that it is not a quick or uncomplicated way to make money and the perception of crocodile farming as an easy system where a large number of crocodiles are thrown in a pen together is incorrect (Bothma & Van Rooyen, 2005). As discussed previously, recent research has suggested that inappropriately high stocking densities reduce production, and a substantial investment must be made into appropriate housing facilities (Bothma & Van Rooyen, 2005).

2.9.2 Genetic variation in commercially farmed crocodiles

Genetic improvement, although not widely utilized, could be used to make improvements by selecting from the stock already available. Isberg *et al.* (2003) studied breeding objectives for genetic improvement in the saltwater Crocodile, with skin and meat as the primary products of production. The study concluded that the following factors be incorporated into breeding objectives in order to maximise production: survival rates, hatchlings/female/year, feed conversion efficiency, and finally age to slaughter (Isberg *et al.*, 2003). Flint *et al.* (2000) studied genetic variation in the Nile crocodile in the North West Province of South Africa and concluded little is known about Nile crocodile genetics in captivity or the wild, unfortunately the results had no standard to be compared to. The genetic implications of random wild harvest, as well as the depletion in numbers of crocodiles in the wild in



recent years, have not been assessed; but there is a potential lowered variability (Flint *et al.*, 2000). Low genetic variabilities could be attributed to certain factors such as genetic drift, bottlenecking, or the founder effect. It is believed that low variation could be partially attributed to other factors as well, such as adaption to a continually stable environment in past years. A final potential cause of reduced variation could be poor husbandry practices, and subsequent inbreeding and loss of heterogeneity (Flint *et al.*, 2000).

2.9.3 The value of farming crocodiles commercially

There are no reliable estimates of the monetary value of crocodilian farming worldwide, prices and values differ with species, type of skin, and quality of skin. Classic skins (like that of the Nile crocodile or Saltwater crocodile) fetch a greater price than those of the caiman for example (MacGregor, 2006; Bothma & Van Rooyen, 2005; www.iucncsg.org [1]). In 2013 the value of classic skins marketed through the luxury brand sector in international trade was estimated at more than US\$100 million annually for raw skins and more than US\$200 million in the form of leather (www.iucncsg.org [7]). In 2004 a Saltwater crocodile skin could be sold for US\$9/cm belly width for a first-grade skin, or US\$360 for a 40cm skin (Hawkins & Huynh, 2004). In 2011 a first grade Saltwater crocodile skin could be sold for >\$AUD25/cm belly width (Manolis & Webb, 2011). Caldwell (2017) reported the US\$ value of American Alligator (*Alligator mississippiensis*) and Spectacled caiman (*Caiman crocodilus fuscus*) skin exports between the years 2006- 2015 (Tables 3(a) & 3(b)). In 2015 the value of an exported American alligator skin from the USA was US\$275.6 (re-import value was US\$391.5). The 2015 value of a re-exported Spectacled caiman skin originating in Columbia was US\$93.0 (Caldwell, 2017).

Commercially the Nile crocodile (see Table 3(c)) has fared well with 80 000 skins traded worldwide in 1993, followed by an increase from 140 000 to 170 000 per year from 2 000-2 010, and finally an average of 245 000 skins were traded globally from 2011-2015 (Caldwell, 2017; Caldwell, 2007; Collins, 1995). The approximate annual gross revenue for crocodile meat and skins from a production unit of 3 509 crocodiles was R2.6million/year in 2005 (Bothma & Van Rooyen, 2005). Skins sold on international markets are to be tagged with plastic CITES tags (in tail skin) for authenticity; both import and export permits are required for trade in crocodile skins (Bothma & Van Rooyen, 2005). CITES classifies the Nile crocodile under appendix II in South Africa, meaning only skins produced by captive populations are to be sold internationally (Blessing *et al.*, 2014; Bothma & Van Rooyen, 2005). The information on these tags encompasses the following: unit of production, year of production and the tag number (Bothma & Van Rooyen, 2005).

When crocodile farming was new to South Africa, the meat was seen as worthless and was fed back to crocodiles, but recent years have seen a growing interest in the meat both locally and internationally. Tail meat is sold for R25-R50/kg, and trunk meat at R8-35/kg (Bothma & Van Rooyen, 2005). Selling the meat internationally yields even higher prices than this; for this to be viable however, on-farm abattoirs are required that must meet the strict requirements of the meat export market. Sick or infertile adult crocodiles are not to be sold to other crocodile farmers or butcheries, such animals are usually sold to tourism-agencies or humanely discarded of (Bothma & Van Rooyen, 2005).



Table 3(a) Direct, commercial exports of *Crocodylus niloticus* skins from producer countries, 2006-2015. Table adapted from Caldwell, 2017

Country	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Botswana	0	320	374	1626	1500	1800	1000	4000	4500	4400
Brazil	0	0	0	0	0	0	0	0	0	0
Ethiopia	727	594	492	0	4	77	400	0	0	6
Israel	0	0	1	2	0	0	100	0	0	27
Kenya	8710	6354	4504	4283	4309	4180	6903	6332	5300	6504
Madagascar	6660	5500	2640	2450	0	0	0	0	3	154
Malawi	698	1350	3370	2603	399	1580	6063	5373	2784	6246
Mali	0	0	107	0	0	15	0	0	0	0
Mauritius	83	180	189	100	0	338	150	102	100	
Mozambique	2021	179	566	0	2449	18788	7234	22700	10781	11161
Namibia	305	0	0	600	2	200	800	1103	1458	2127
Senegal	2	0	1	0	0	0	0	0	0	7
South Africa	23542	30514	37627	25050	53329	57298	77473	73032	121057	59638
Sudan	0	0	2	0	20	0	0	0	0	7
Tanzania	1100	1556	1784	1365	601	475	1209	1379	1287	1294
Uganda	300	0	290	0	500	0	405	400	515	600
Zambia	40457	37305	28197	43655	23717	37584	15331	45368	44233	43926
Zimbabwe	71616	64490	81554	67350	80995	90533	88421	115499	90828	115499
Total	156211	148342	161698	149084	167825	212796	205489	275288	282846	251596

Note: table units encompass all direct commercial trades including whole skins, live animals and whole skin equivalents. This table encompasses trade from all sources (i.e.: wild, ranched or captive bred), see Caldwell (2017) for more detail.

Table 3(b) Table sourced from Caldwell, 2017. Reported US dollar value of *Alligator mississippiensis* skins (per skin) exported and re-imported by the United States, 2006-2015

	, ,		•	,		•				
	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Exports	177.9	232.9	242.2	193.3	136.0	167.5	194.9	241.1	261.6	275.6
by USA										
Re-	193.5	253.4	254.8	394.7	236.9	245.7	260.1	407.5	444.15	391.5
imports										
by USA										

Source: United States annual reports to CITES

Table 3(c) Table sourced from Caldwell, 2017. Reported US dollar value of *Caiman crocodilus fuscus* skins (per skin) originating in Colombia and imported by the United States, 2006-2015

(Re)-	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Exporter										
Columbia	50.8	54.4	52.5	72.2	65.3	73.4	76.6	79.1	96.8	93.0
European	34.5	-	-	87.3	54.9	71.0	99.9	61.6	58.4	78.4
Union										
Mexico	31.2	50.0	36.3	38.0	34.5	33.0	34.0	23.4	23.7	20.7
Singapore	46.7	46.1	44.3	47.3	50.5	46.2	58.1	47.2	70.9	71.4

Source: United States annual reports to CITES



2.10 Injuries, diseases and other conditions

With the advent of crocodile farming, came a brand-new veterinary field of dealing with crocodilian diseases and parasites. Means of control have been established for commonly encountered issues in captive crocodile populations (Beyeler, 2011; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002). The majority of diseases encountered in such populations are opportunistic and come about as a result of poor hygiene, improper feeding, poor temperature control and the resultant stress reactions which lower the animals' immunity (Beyeler, 2011; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002). Illness and injury monitoring should occur as regularly as possible, especially in pens with adult crocodiles. Strains on health are known to negatively affect feeding and reproductive activities (Verdade *et al.*, 2006; Bothma & Van Rooyen, 2005). Injured crocodiles are to be treated as soon as possible, when this occurs the animals should be blind-folded, and their jaws taped shut. Stress and disease susceptibility are greatest in the first year of life, survival rates are approximately 70%. Farmers themselves may not see this as economically ideal, but it is a substantial achievement when one considers the wild survival rates can be as low as 1% (Brien *et al.*, 2007; Bothma & Van Rooyen, 2005).

Chronic stress can be deadly in the early days of life, farmers who claim to have a 100% survival rate are likely not counting eggs removed from the incubators for structural issues, and therefore the supposed 100% encompasses only the best quality eggs they produce (Brien et al., 2007; Bothma & Van Rooyen, 2005). Inappropriate stocking rates, loud noises, excessive handling, and early dietary changes should be avoided if young crocodiles are to thrive (Beyeler, 2011; Brien et al., 2007; Huchzermeyer, 2002). Salmonella is the most commonly encountered issue, these bacteria are known to thrive in crocodilian systems without any harm to the animal; but if the animals' immunity is challenged in some way (and therefore weakened) these bacteria become problematic and potentially life threatening (Bothma & Van Rooyen, 2005). Fungal diseases are the most commonly encountered issues in hatchling crocodiles (Davis, 2001). Disease monitoring via the noting of behavioural changes or an increased number of deaths in young crocodiles is an important production factor. Staff working daily with crocodiles should be trained to notice and record such occurrences (Beyeler, 2011; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002). Some diseases known to affect units in Zimbabwe and South Africa are: viral and bacterial hepatitis, viral enteritis, pox virus, septicaemia of a bacterial nature, ophthalmia, chlamydiosis, and fungal infections. Parasites such as leeches, worms and nematodes have also been encountered in farming operations. Although many of these issues have formulated-treatments in the market, there are issues where prophylaxis and maintenance of strict hygiene protocols is the only solution (Bothma & Van Rooyen, 2005; Huchzermeyer, 2002). Social hierarchies, poor housing or feeding, poorly maintained hygiene, and inappropriate temperature regulations all cause reduced immune function and therefore increased disease susceptibility; especially where opportunistic diseases are concerned. Proper housing and management, along with strict biosecurity monitoring systems are the best approach to minimizing disease issues in farmed crocodile populations (Beyeler, 2011; Bothma & Van Rooyen, 2005; Huchzermeyer, 2002).

2.11 Crocodile skin

2.11.1 Skins: the primary product of commercial crocodile farming

Skin is the primary product of crocodile farming, different crocodilian species yield different skins, and these are of varying value (MacGregor, 2006). Crocodiles are usually of an ideal size for slaughter at the age of 2-3 years. This can vary depending on farm location, management and diet (Beyeler, 2011). First grade skins supply luxury markets internationally and are used by many popular brands for leather shoes, bags, belts and watch straps for some well-known brands like Gucci, Hermes,



Louis Vuitton and Rolex (Tosun, 2013; Beyeler, 2011; MacGregor, 2006; www.fao.org). Nile crocodile skins are classified as "classic leather" on the international market and fetch a reasonable price (Bothma & Van Rooyen, 2005). Skins are processed in the following steps: skinning, skin preparation via flaying, measuring and grading (usually on a light table), salting, folded and packaged into woven plastic bags, transported, tanned, coloured, and finally worked into marketable products (Bothma & Van Rooyen, 2005). The skill level of the skinner will determine the quantity of wastage, and therefore the sizes of the skins presented to the next stage of processing (Mpofu *et al.*, 2015). Salting is an equally crucial step and is essential for the prevention of bacterial or fungal infections of the skin, and scale decay or slipping. Substandard salting practices cause shrinking of skins by up to 16% (Mpofu *et al.*, 2015).

Crocodile skin consists of a network of scales, or scutes, in multiple shapes and sizes depending on body location (Beyeler, 2011; Buenviaje, 2000; www.iucncsg.org [6]). Belly scales are square and flat, flank and neck scales are round with raised bony centres, and finally the back and tail has pronounced raising in the scales (Bothma & Van Rooyen, 2005; www.iucncsg.org [6]). The bony deposits in scales are called osteoderms, they have rich blood and nerve supply and assist the transfer of heat to and from the body (Bothma & Van Rooyen, 2005; Huchzermeyer, 2003; Buenviaje, 2000; www.iucncsg.org [6]; www.fao.org). The soft and malleable belly scales on the other hand have no osteoderms, making this area of the skin the most highly valued (Beyeler, 2011; Bothma & Van Rooyen, 2005; www.fao.org). Skin quality can be defined as the hide properties of shape, thickness, and scale pattern uniformity (MacGregor, 2006; Bothma & Van Rooyen, 2005; Isberg et al., 2003). It was concluded in the study by Manolis & Webb (2011) that farmed saltwater crocodile skins are thinner than those of their wild counterparts, due to their higher growth rates in the early years of life. These thinned skins are more damage susceptible in both rapid growth periods and social hierarchy fighting interactions (Manolis & Webb, 2011; Isberg et al., 2003). Belly width and quality are the primary determinants of skin selling price, with the optimum width between 32 and 42cm (Beyeler, 2011; Bothma & Van Rooyen, 2005; Isberg et al., 2003; www.fao.org). Legal international trade in crocodile skins is regulated by a system of import permits and tagging of every skin with a unique numbered non-reusable tag (www.iucncsg.org [1]).

2.11.2 Grading of crocodile skins

The grading systems for crocodile skins have become stricter in recent years with the growth of the market. The skins of the Nile crocodile and American Alligator are of particular popularity (Mpofu *et al.*, 2015). Developing countries tend to struggle with the production of near-perfect skins. Issues such as physical damage, nutritional defects, and poor skill of skinners and tanners are typically encountered at a greater frequency in such countries (Mpofu *et al.*, 2015). Each downgrade of skins entails a 25% loss in value, in order to preserve the grades of skins international housing and nutritional requirements must be met (Mpofu *et al.*, 2015; Isberg, 2007; Buenviaje, 2000). Mpofu *et al.* (2015) proposed that the greater stocking densities used to maximise the number of skins produced, has led to downgrading of the skins as a result of aggression and territoriality related damage.

Crocodilian skins are graded according to both extent and severity of physical damage to the skin. Defects of the skin can range from simple blemishes, bite or scratch marks, abrasions, deformities in the scale patterns, and knife holes (Beyeler, 2011; Isberg *et al.*, 2003). Skin gradings have varied between studies; some grade their skins from 1 (being the best quality skins) till 4 (worst quality skins), and others from 1 till 5 (Beyeler, 2011; Manolis & Webb, 2011; Isberg *et al.*, 2003; Buenviaje, 2000; www.rojeleather.com). First grade skins are those devoid of imperfections, the grade is diminished down to fourth grade by the extent of imperfection occurrences (Isberg *et al.*, 2003; Buenviaje, 2000).



According to Manolis & Webb (2011) skin grades can be summarised as follows: first grade skins have no defects or small defects on the tail and throat areas only, second grade skins are those with minimal belly defects (located either on the top half or bottom half of the belly, or the left or right sides only of the belly) but more severe throat and tail defects; and finally, third grade skins are those is where there are significant belly defects. Fourth grade skins are the worst quality skins produced (sometimes these crocodiles are automatic culls) and often don't make it to the international fashion market, but may be utilized in locally produced products for tourists, i.e.: curio markets (Manolis & Webb, 2011; Isberg, 2003; Buenviaje, 2000; www.rojeleather.com). It is estimated that only approximately 30% of skins meet first grade requirements. This downgrading can be accorded to the employment of poor husbandry and management techniques, specifically the design of pens and stocking densities (Isberg et al., 2003). Skin imperfections are numerous, and classification of defects can differ between production systems (Manolis & Webb, 2011; Buenviaje, 2000). Some examples of skin imperfections with potential causal factors following in brackets are as follows: scars (fighting), cuts (skinning), wrinkles (cull process), double scaling (impaired GR), scale slip (extreme temperature fluctuations), and fungus/brownspot (fungi/bacterial growths of the skin) (Manolis & Webb, 2011).

2.12 Crocodile meat

Crocodile meat is the main by-product of crocodile farming; the CSG estimates the production of meat from 1990-2005 to be approximately 400 tons/year primarily from three species: the Nile crocodile, the Siamese crocodile, and American alligators (Tosun, 2013; www.iucncsg.org [1]). The recent interest in crocodile meat as somewhat of a delicacy has improved crocodile farmers' economic outputs. The primary focuses of crocodile producers are skin quality, and the newly introduced meat quality and growth characteristics (Tosun, 2013). Crocodile meat is easily marketed as a healthy meat, with a low sodium and high unsaturated fatty acid content (Tosun, 2013; Hoffman *et al.*, 2000).

2.12.1 Ideal crocodile killing methods

Crocodiles are ideally killed by electrical stunning of the brain and severance of the spinal cord; spinal severance is not permitted prior to stunning. The stun permits a final opportunity to check that the animal is of size and quality for slaughter, with minimal or at least partially healed skin irregularities (Beyeler, 2011; Bothma & Van Rooyen, 2005; Huchzermeyer, 2003). Feed is restricted for the week leading up to slaughter so as to prevent regurgitation during the culling, or at the time of skinning. During the harvest for slaughter, prolonged handling can lead to a build-up of lactic acid in the muscle, reducing meat quality (Bothma & Van Rooyen, 2005). Capturing techniques will also affect stress felt by the other crocodiles in the pen, this can cause running over one another and biting, resulting injuries reduce skin quality. Nearly all crocodile producers use an electric stunner, immobilising the animals for 2-3 minutes and therefore reducing issues such as mentioned above (Bothma & Van Rooyen, 2005). Within ten minutes of death, the carcass should be hanging for bleeding out. This is accomplished by hanging the crocodiles by the tail. The carcasses should be washed of any faecal matter, blood, or mucus remaining on the body including inside of the mouth. There are few abattoirs licensed to deal with crocodile meat, it is important that the farm be as close to such an abattoir as possible for the sake of meat quality, as transport over long distances can be detrimental to this (Bothma & Van Rooyen, 2005).

2.12.2 Crocodile meat quality-regulations

Crocodile meat as a product is seen as a delicacy in many countries, but the reality is that there are minimal regulations in place compared to other meat producing farming systems (Magnino



et al., 2009; Bothma & Van Rooyen, 2005). Magnino et al. (2009) analysed some of the biological risks involved with the consumption of reptile meat products. Issues encountered in farmed crocodiles include bacterial infections (Salmonella and Vibrio species), parasites (Spirometra, Trichinella and Gnathotoma), and toxins (Manolis & Webb, 2011; Magnino et al., 2009). Spirometra and Trichinella can be inactivated by freezing reptilian meats (Magnino et al., 2009). Of the listed issues, Salmonella is the major issue faced. Particularly in farming situations where chicken is the primary feed available, or crocodile meat infected with Salmonella could potentially be transferred back into the population when they are fed back into the system (Magnino et al., 2009). The concluding remarks of the study identified testing procedures as an essential implementation for the future of crocodile meat production and sale into the meat-market. This is especially important with any crocodile farm feeding chicken as their primary protein (Magnino et al., 2009).

2.12.3 Crocodile meat characteristics

Hoffman *et al.* (2000) studied the meat characteristics of the Nile crocodile and found a dressing percentage of approximately 56.5% (compared to the 63.3% approximated for *Alligator mississippiensis*), with the tail comprising 33% of empty-carcass weight. The tail can be utilized for fillet pieces or tail-cutlets, with the rest of the usable carcass sold as lower-value product to restaurants or exported. Their findings indicated crocodile meat being characteristically low in iron, sodium and magnesium contents when compared to other meat-producing species such as beef and chicken (Hoffman *et al.*, 2000). Isberg *et al.* (2003) stated that a yield of 4-5kg of boneless meat could be attained from a 1.5m long crocodile (1.5kg tail and 2.5kg body meat). Crocodile meat quantity is thought to be inversely proportional to skin production, producers should be cautious not to overemphasize either of these traits too strongly for fear of compromising the other (Bothma & Van Rooyen, 2005; Isberg *et al.*, 2003). Colour variations in Nile crocodile meat were noted by Hoffman *et al.* (2000), with the neck and tail sections having the lightest meat, the leg meat was darker in colour. Neck meat is the leanest cut from a crocodile carcass, with the highest protein content both before and after cooking. The tail and legs were found to have higher fat contents than the neck (Hoffman *et al.*, 2000).

2.13 Crocodile behaviour

Crocodilian behaviour is complex, and there are aspects of their behaviours and social interactions that are not fully understood; with much of the information available based on studies involving wild populations (Brien, 2015; Dinets, 2013; Lang, 1987). Studies emphasize the relationship between behaviour and management, highlighting comprehension of how management affects behaviour, and behaviour affects management as essential for successful stocking programs (Brien, 2015; Lang, 1987). Behaviour involves both physical and chemical actions in the body, i.e.: growth and reproduction are hormonally controlled, inciting the related responses of feeding and competing for feed, or mating and seeking out mates. Crocodiles are ectothermic, requiring heat sources external to their bodies to maintain their body temperatures, appetites and metabolic rates. Temperature maintenance is therefore essential for the health, growth and reproduction of crocodiles (Brien, 2015; Tosun, 2013; Bothma & Van Rooyen, 2005; Lang, 1987; www.iucncsg.org [5]).

2.13.1 Crocodile behaviour in the wild vs. in captivity

Social interactions are an important behavioural activity, and studies involving captive crocodilians have highlighted the differences in social behaviours encountered in these captive animals when compared to their wild counterparts (Lang, 1987). Behaviours mature with age, size and



gender of crocodilians. Wild, juvenile crocodiles have been recorded banding together and forming living-groups; then a disbanding of such groups when competition and dominance behaviours begin to arise due to size divergences; and finally, the formation of territories and mating behaviours when the animals mature (Huchzermeyer, 2003; Lang 1987). Once again it should be noted that wild and captive crocodilians will have differing experiences. Captive animals are obliged to adapt to social hierarchies such that would not be encountered in the wild (Brien et al., 2013; Webb et al., 2013; Huchzermeyer, 2003; Lang, 1987). Lang (1987) suggested crocodiles born and raised in captivity are more likely to adapt to their circumstances. Provided human activities remain consistent, captive animals will adapt and habituate. One negative behaviour that is unavoidable in crocodile farming situations is the formation of a hierarchy, and the agonistic interactions that ensue. Dominant crocodiles tend to dictate feeding, and areas of pens accessible for smaller crocodiles. This is thought to be species-specific, size dependent, and determined by the densities at which the crocodiles are housed (Brien et al., 2013; Morpurgo et al., 1993; Lang, 1987). The stress endured by the submissive animals can have negative effects on their growth, health, and their ability to behave naturally within their setting. The sorting of animals periodically into groups of similar sized animals is necessary in these situations and can yield a reduction in aggressive behaviours as there is less opportunity for dominance behaviours (Brien, 2015; Webb et al., 2013; Cuijk, 2011; Morpurgo et al., 1993; Lang, 1987).

2.13.2 Forms of communication in crocodiles

Crocodilians utilize various vocalisations/acoustics as a form of communication. Vocalisations include bellowing, roaring, hissing and screaming. The intentions of such vocalisations can vary from warning/threatening another animal, to signalling for a parent crocodile, to signalling distress. Crocodilian postures are of interest as they can spend most of their time being very still, with short energy bursts attributed to anaerobic metabolism, after which a significant recuperation time is required (Dinets, 2013; Lang, 1987). Although crocodiles can remain still for hours at a time, research suggests they are still aware of their surroundings. Posturing, snout-lifting, head slaps, jaw snaps and tail thrashing are some other communicative tools; usually used to express warnings or aggressive intentions. The basking pose of holding the mouth open and head slightly elevated has been suggested as "lookout" or warning pose, or a bluffing attempt in the face of an opponent; as well as a temperature regulation posture (Brien, 2015; Brien *et al.*, 2013; Dinets, 2013; Bothma & Van Rooyen, 2005; Lang, 1987).

2.13.3 The importance of behavioural monitoring in crocodile farming

In captive crocodile farming situations, it is especially important to monitor behaviours and utilize the information gathered to improve management for the sake of encouraging more natural behaviours (Tosun, 2013; Bothma & Van Rooyen, 2005; Lang, 1987). Monitoring of feed activities, aggression, spatial distributions or tendencies, temperature-maintenance activities and potential stress-indicating behaviours allows for the identification and rectification of factors negatively affecting crocodiles in captive rearing situations (Lang, 1987).

In the case of more in-depth monitoring requirements than farm-handlers can provide, automated camera and video surveillance has become an essential tool for behavioural research. Some advantages of this type of recording are: the time over which recordings can be captured and potential for numerous sites of sampling (Rovero et al., 2014). It would be inefficient to have handlers posted continuously around farmed crocodiles, not to mention the stress this could potentially cause the crocodiles, which would also impact their behaviours (Rovero et al., 2014; Martin & Bateson, 2007). The technology requirements of such monitoring are readily available and there are multiple



models boasting various features and specifications according to the users' needs (Rovero et al., 2014).

2.14 Crocodile welfare

Animal welfare standards are continuously evolving and being updated over the years as the understanding of the welfare needs of farmed animals' advances (Mellor, 2016; CFAZ, 2012). Husbandry practices are continually advancing to match the acceptable standards of animal welfare as set out in the national codes of practice for crocodilian farming. South Africa and Zimbabwe's (Nile crocodile) standards are detailed in the South African Bureau of Standards Division (SABS, 2014) and Crocodile Farmers Association of Zimbabwe (CFAZ, 2012) respectively. See Manolis & Webb (2016) for further details regarding standards for different species and producer nations. The CSG-BMP 'living document' (to be reviewed and updated as ongoing research permits) has collated relevant and current information on Best Management Practices for Crocodilian Farming (Manolis & Webb, 2016).

The Best Management Practices for Crocodilian Farming outlines four major approaches utilized to practically assess animal welfare in a scientific manner. Anatomical and physiological assumptions make up the first approach; i.e.: the widely accepted (and scientifically backed) assumption that stunning achieves a more humane culling practice due to pain reduction. The second approach is the evaluation of health correlations; i.e.: measures of body condition, growth rates, survival rates, reproductive success, injuries and disease/parasite incidences are indicative of animal health. The third approach involves biochemical indicators; i.e.: the comparison of corticosterone levels to assess stress. The fourth approach encompasses behavioural surveillance and stimulus response (behavioural outputs towards a certain stimulus); i.e.: activities such as piling, distress calls or dehydration could be considered behavioural responses to impaired health or comfort in an environment. These four approaches can be applied on-farm for a practical assessment of animal welfare, allowing improvement and updating of management practices.

The five freedoms have been the accepted and internationally published welfare standards since 1993/1994 and are still in use currently (Mellor, 2016; CFAZ, 2012). However, recent studies have shed light on some inadequacies and misinterpretations of this model; namely the misinterpretation of the "freedoms" as absolutes rather than guidelines for minimizing stresses (Mellor, 2017; Mellor, 2016). The five domains model is thought to be an improvement of five freedoms, developed by Mellor and Reid. Both models are intended as a method of assessing a management system with the intention of guiding welfare improvement, rather than a set of rules to be followed to a tee. The five domains (summarised in Table 4) are: "Nutrition", "Environment", "Health", "Behaviour" and "Mental state". Overlap between these domains is to be expected, and only through the understanding of these interactions can changes be implemented toward the betterment of farmed animal welfare (Mellor, 2017; Mellor, 2016). The five domains model does not define specifics (in terms of housing or density for example) rather it provides the tools for comprehensive assessment of animal welfare. When applying this model to a species of interest it is essential to incorporate knowledge of species-specific physiologies and behaviours, as well as the concurrent physical and social environments experienced (Mellor, 2017).

The five domains model defines both negative ("welfare compromise") and positive ("welfare enhancement") welfare experiences. The negative experiences can be divided into survival-critical negative effects (those essential to life; such as: food, water and environment), and situation-related factors (such as health maintenance and behavioural expressions). This is an important distinction as the survival-critical factors can ideally be temporarily neutralized (primarily by human intervention in farming systems), whereas the situation-related factors can be transformed into positive experiences (in the form of the ability to express behaviours considered rewarding for the animals) depending on



the animals' circumstances. These two types of factors can interact when a survival-critical factor causes discouragement of situation-related factor behaviours (Mellor, 2016).

Essentially, the aim of welfare management is the reduction of survival-critical negative effects to tolerable levels and the encouragement of the implementation of improved environments so as to allow positive interactions, interests and self-confidence formation in farmed animals (crocodiles included). It has become obvious over the years that ensuring the survival-critical effects are met is not sufficient. The need to "thrive" is becoming a part of current welfare systems, this is where the situation-related factors come into play (Mellor, 2016).



Table 4 Table sourced from Mellor, 2016. Depicts an abbreviated version of the Five Domains Model, for more information refer to the study



3. MATERIALS AND METHODS

Ethical approval for this study was granted by the University of Pretoria Animal Ethics Committee, project number EC070-17 (Annex G).

3.1 Animals, housing and climate

3.1.1 Animals and housing

In May-November 2017, two hundred and sixty-one early grower Nile crocodiles (*Crocodylus niloticus*) provided by a commercial crocodile farm in South Africa were used to assess different stocking densities employed in current commercial crocodile production. All of the crocodiles in this study were hatched on the farm and raised similarly in terms of diet, housing and general animal husbandry. The animals were nearing 15 months of age (hatched January-February 2016) when the trial began and were selected from a group of crocodiles of similar age based upon their total body lengths, to ensure as balanced a starting point as possible. These total body lengths ranged from 74.5cm to 111cm in length.

The layout of the house assigned to the trial was such that the 261 crocodiles were randomly allocated to eight pens of comparable size (approximately 26m² each), all in the same house. The number of crocodiles assigned to the pens varied, allowing the assessment of the effects of stocking density on production and behaviour over a 6-month period (Annex F, plate 1-2). See Figures 3.1 and 3.2 for the house and individual pen dimensions. The use of this number of animals ensured a realistic comparison of the current industry-practises and allowed the house to be filled with trial-only animals.

Three stocking densities were tested based upon current farming practices in South Africa and Zimbabwe (CFAZ, 2012), and recommendations from the owner of the farm. The highest stocking density (Annex F, plate 4) was based on current high-density recommendations for commercial farming practices involving crocodiles of this age and size, and the lowest density (Annex F, plate 5) would likely be considered by most farmers as a waste of farming space. The eight pens were divided as follows: three high density pens, three low density pens, and two medium density pens.

Sixty-three crocodiles were assigned to each of the highest density pens, the medium density pens were assigned 21 crocodiles each, and the three lowest density pens had 10 crocodiles each. The space allowances for the above mentioned, from highest to lowest stocking density, are as follows: 0.43m^2 per crocodile, 1.24m^2 per crocodile, and 2.60m^2 per crocodile. It should be noted that the crocodiles were not moved from their assigned pens throughout the 6-month trial period, the aforementioned space allowances were designed not only to compare densities but also to be sufficient in allowing the crocodiles to remain in the pens for the full 6 months when considering the young crocodiles would likely grow during this trial period. Figures 3.1 and 3.2 illustrate the layout of the trial house and the 8 similar pens within the house. The ponds were treated with potassium permanganate for the first week after placement in the trial house (Annex F, plate 6). The water treatment was a standard procedure used on the farm. The potassium permanganate acted as a disinfectant; simultaneously allowing the crocodiles a convenient, if fleeting, opportunity to hide in the water (which took on a dark purple-brown colour) where they could not be easily seen when submerged for the first week in their new surroundings.

The pen floors consisted of a smooth concrete, with tiling on the inner pen walls. A water body ran through the centre of each pen which covered 26% of the pen area, the water depth at the centre of the pond was 0.16m (Annex F, plate 3). The dome shaped roof was covered by a sturdy, white (non-translucent) weather proof plastic (Annex F, plates 1-2). The house contained a walkway situated along the house-midline overlooking the pens to allow easy access to each pen, as well as access to the cameras which were placed around the house to monitor animal behaviour (Annex F, plate 2).



Human presence was minimized so as not to influence the crocodiles stress responses any more than was necessary. Access to the pens was granted for the activities of feeding, cleaning, faecal collections (coincided with feeding or cleaning times to minimize human presence in the house), and weekly time-lapse data collections (which consisted of a switch of the memory card for each camera placed in the house, and a check for battery levels).



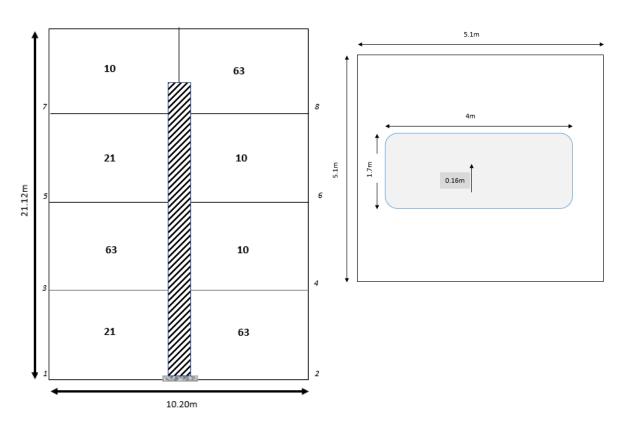


Figure 3.1 Schematic of trial house, including house dimensions, pen numbers (outer edge of diagram), and the number of crocodiles in each pen. Not to scale.

Figure 3.2 Schematic of pen layout with lengths and widths of the pen and pond, as well as the pond depth. Not to scale.

3.1.2 Processing and handling

Pre-trial processing consisted of the capture and securing shut of each crocodiles' jaw with a thick elastic band (Annex F, plate 7). The crocodiles were of an easily manageable size at the beginning of the trial, and stunning was not required at this stage. Each crocodile was microchipped with an Allflex*-brand microchip (Annex F, plate 14), and tissue samples were attained using a sampling gun supplied by Allflex* (Annex F, plate 10). The tissue samples were collected from the first single scute of the tail, creating a hole in the scute which doubled as a tagging hole (Annex F, plates 11-12). These tissue samples were consigned to Allflex* for future use by this company in unrelated genetics-based studies. Each crocodile was tagged using cable ties in the tail-scute hole mentioned above; these tags were colour coordinated according to which pen they were assigned (Annex F, plate 13). Once the tag had been securely placed, the tail of each cable tie was cut off, and a disinfectant spray (Betadine spray) applied to the tagged area of the tail. Various morphometric measures were recorded for



growth assessment, and skin analyses were performed on each animal which included taking a digital picture (Sony DSLR $\alpha 230$) of the crocodiles' belly skins for later referral if needed. Crocodiles with particularly severe skins or injuries were rejected from the selection for the trial. Some crocodiles had teeth that protruded out from their maws, this was seen as a potential damage causing characteristic and so these teeth were clipped before the crocodile was allocated to a pen (Annex F, plate 16-17). Finally, each crocodile was delivered to the pen to which they were assigned via a stratified randomisation.

The post-trial processing consisted of the stunning (Annex F, plate 40) and capture of each crocodile (crocodiles had reached a size where stunning was necessary for handler safety), taping shut of each animals' jaw with the aforementioned thick elastic bands, identification of the animal via a microchip scanner supplied by the company Allflex* (Annex F, plate 15), and a re-recording of the morphometric measures and skin analyses. Each crocodile was marked on the head with a temporary non-toxic white paint after it had been processed at the end of the trial, and placed back into its pen (Annex F, plate 41). On day 119 of 188 in the trial a collection of swab samples were collected, from pens and crocodiles, when the crocodiles began presenting illness (Annex F, plate 36-38).

Genders could not be confirmed, even post-trial, as many of the animals were too small and it was agreed that this would be stressful and potentially painful for the young crocodiles. The random allocation of the crocodiles into pens at the beginning of the trial should have yielded an equal sex ratio between pens (female:male)^{pen1} = (female:male)^{pen2} = ... = (female:male)^{pen8}. These are the justifications for avoidance of this measure in this trial.

3.1.3 Daily recordings

Daily data collection forms were renewed on a weekly basis, each pen had a clipboard assigned to it with the forms to be filled out daily (Annex A). These daily recordings included: feeding and cleaning schedules; feed measures (kg feed fed, and kg feed waste collected); the confirmation of faecal samples by way of recording the weight in grams of each sample and the time of day it was collected (either the morning or the afternoon collection); various temperature measures; and time fluctuations should the farms schedule occasionally not allow the recordings at the usual specified time of day.

A thermo-hygrometer in the house monitored temperatures and humidity (Annex F, plate 29), and daily recordings of floor and water temperature were collected for each pen using a handheld thermometer gun (Annex F, plate 30). The feeding and cleaning schedules followed that of the farms current system and remained unchanged throughout the trial period. To maintain the comfort and socialization activities of the crocodiles in the study, the personnel attending the trial house were kept as consistent as possible. This allowed the animals to adapt not only to their surroundings but to the personnel they encountered daily. The trial was intended to be non-invasive as far as possible, faecal collections and camera surveillance were used to ensure the crocodiles were not unnecessarily stressed. Physical handling and measures/sampling were limited to pre- and post-trial, and in the instance where an illness was suspected and had to be tested for.

3.1.4 Climate recordings

Two weather-data recording products were utilized in this trial for the measurement of temperatures and humidity in the house and in each pen: a Kistock miniature thermo-hygro datalogger (Kimo instruments: KH120), and a standard hand-held IR (infrared) thermometer (ST653), ordered through ASSTech Process Electronics and Instrumentation.

The temperature and humidity datalogger was housed in a protective casing with a magnet for easy mounting; and capable of measuring temperatures from -20 to 70°C, and humidity of 5-95% RH. The memory capacity for the logger was 50000 points of record, making it more than capable of capturing hourly recordings over a 6-month trial period. Configuration and report outputs can be easily attained as the logger has a built in USB connector, and free online data processing software. The thermo-hygro datalogger was placed in the trial house for the duration of the trial, set to record hourly temperatures and humidity. The datalogger unfortunately malfunctioned early in the trial, and the manufacturers had to be contacted. After some assistance the thermo-hygro datalogger was again set up in the house and successful recordings began mid-July till the end of the trial. The batteries were replaced twice during the trial, indicating a further issue with the device as according to its manuals a single battery should have lasted closer to a year at the recording interval it was set at. Nevertheless, this data was included in the analyses, and supplemented with weather data requested from a weather station nearby. These external weather recordings were requested and received from the South African weather services (SAWS) for the farms GPS coordinates. Hourly temperature and humidity data from SAWS were used to complement the in-house climate data recordings attained from the hygrometer.

The handheld IR thermometer is capable of measuring temperatures ranging from -35 to 535° C (resolution 0.1° C). An adjustable emissivity range allows recording from multiple surface types. The handheld recorder was used daily, at midday (warmest time of the day), in every pen to measure temperatures attained by the cement floors and water bodies and emissivity adjustments had to be made between each change of material measured.

3.2 Feed Intake

Feeding was carried out on every Sunday, Tuesday, and Thursday during the trial (Annex F, plate 32); and cleaning on every Monday, Wednesday, and Friday of the trial (Annex F, plate 33). This system was developed by the farm owner to ensure that every feeding day was followed by a cleaning day, thereby ensuring the maintenance of hygiene in the pens (and ponds in particular). All crocodiles were fed the same diet throughout the trial. The diet was the current grower diet that the farm fed crocodiles at this stage of production (prepared on the farm) and consisted of a mix of ground up chicken and nutritional premixes (Annex F, plate 31). Continuous assessments of the amount of feed fed and the feed waste collected for each pen allowed weekly adjustments of the feeding quantities, ensuring there was sufficient feed available to satisfy the requirements of the trial crocodiles. This feed adjustment was also a typical practice on the commercial farm, and so did not diverge from their usual regime.

3.3 Growth



Each selected crocodile was weighed in a holding crate, on a large standing scale (Annex F, plates 8-9). The following morphometric measures (depicted in Figure 3.3) were recorded for each crocodile: total body length (TBL: from the tip of the snout to the tip of the tail), snout vent length (SVL: from the tip of the snout to the caudal margin of the cloaca), and finally belly width (BelW: the width of the belly from the third button-scale of the belly on each side of the crocodile). After recording these morphometric measures, Fulton's formula was used to calculate a body condition index/score for each crocodile (K = W/L³ x 10³; where K is the condition score, W indicates weight, and L indicates length) (Manolis & Webb, 2016; Mazzotti *et al.*, 2012; Zweig, 2003). It should be noted there were two sets of Fulton's results analysed: one where the total body length measure was incorporated as recommended by previous studies using this equation for crocodilians/fish; and another in which snout vent length was used. Previous studies (Mazzotti *et al.*, 2012; Zweig, 2003) used snout vent length for this calculation to avoid inaccuracies arising from missing tail ends.

Only a fraction of the crocodiles in the current study were recorded with missing tail ends, and although it was not expected that the results of these two Fulton's calculations would be significantly different, the calculation was repeated using TBL and SVL to ensure precision. A 1 metre long metal ruler was placed on the table top where processing occurred, so that the crocodiles could be carried and placed directly over the ruler for ease of measuring. A percentage of the crocodiles were over a metre long, for these crocodiles a flexible tape measure was used to measure the last few centimetres. This flexible tape was used for the snout vent length and belly width measures as well. Throughout the trial, the amount of feed fed, and feed waste collected was recorded to determine the amount to feed to each pen, and to follow the intakes of each pen for comparison to the growth data. Refer to Annex B for the data sheet used for growth-measure recordings.

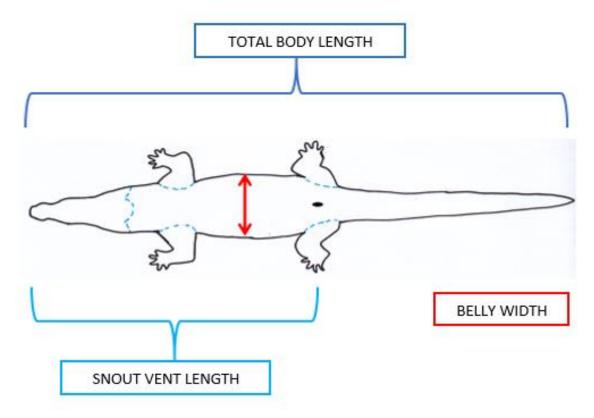


Figure 3.3 Illustration of the various morphometric measures used to assess crocodile growth

3.4 Behaviour



Eight cameras (Bushnell Trophy Cam Aggressor HD) were assigned, each to a pen, for time-lapse image recordings (Annex F, plate 2). Sixteen 32GB secure digital memory cards were alternated, two per camera, throughout the trial to ensure the in-house data-collection time was minimized. The cameras were placed on brackets attached atop retractable poles, allowing the cameras to reach a height of 3.34m from the ground level of the pens. These camera-poles were secured to the walls of the pens a distance of 1.48 m from the walkway; this was the point where maximum height could be reached due to the sloping of the dome-shaped roof. As shown by Figure 3.4: each camera faced the pen on the opposite side of the walkway, this allowed a maximum area of the pen to be captured in the time-lapse images. An estimated 10% of each pen was "cut-out" of the time-lapse images even with this placement of the cameras, due to the cameras frame-capabilities this was a tolerable loss. Each pen had a camera allocated to it, on time-lapse settings so that hourly images were captured. These Bushnell cameras also had thermal sensors, and although the crocodiles' movements did not activate the thermal sensors, the movements of any people in the house did.

Although hourly images were captured for each pen throughout the trial period, analysing the full data set would have been impractical. It is due to this fact that a stratified randomisation was performed, allowing the random selection of six images per day per pen for analysis. This stratification ensured that even though every image could not be assessed, every time slot would be analysed for every pen at some point throughout the recording period. Each time-lapse image was given an identification code consisting of the pen number, date, and capture-time of the image. To compare the behavioural data by density, and to the other data sets collected, it was determined that important measurements would involve a quantification of contact/piling (Annex F, plate 34) and aggression behaviours. Parameters of how many animals were involved, or not involved, in contact and piling behaviours in each pen was recorded. For clarification it must be noted that contact and piling were related, as crocodiles piling are technically in contact with pen-mates. The distinction when these two variables were recorded lies in the classification of piling as either: a pile of crocodiles (as can be seen in Annex F, plate 34), or when less crocodiles were involved piling was classified as the crossover/intersection of crocodile bodies. Contact on the other hand was defined as crocodiles in close proximity to one another, with only a small area of bodily contact (i.e.: positioned side by side, with no overlap of body parts). These recordings were further divided up into land and water recordings (see Annex D). The aggressive behaviours unfortunately were not consistent enough in the time-lapse data for analysis. It became clear that had there been sufficient time and manpower, these aggression behaviours would be better analysed with in-depth video analyses.

Some other recordings that were added to the behavioural data spreadsheet (Annex D) that should be noted before reviewing the results section are: human presence in the image, water clarity, and some general comments. Human presence was a simple yes (1) or no (0) recording where if there was a person in the image or within 30 minutes of the image, then it could be assumed that this could have had an effect on the behaviours seen. This recording was also useful to track the feeding/cleaning schedule, and monitor the workers entering the house. Water clarity was a simple clear (1) or murky (0) score allocated to each time lapse image based upon the clarity of the water. The comments column was used to track mortalities, instances of aggression, and divergences from the regular trial-house schedule.



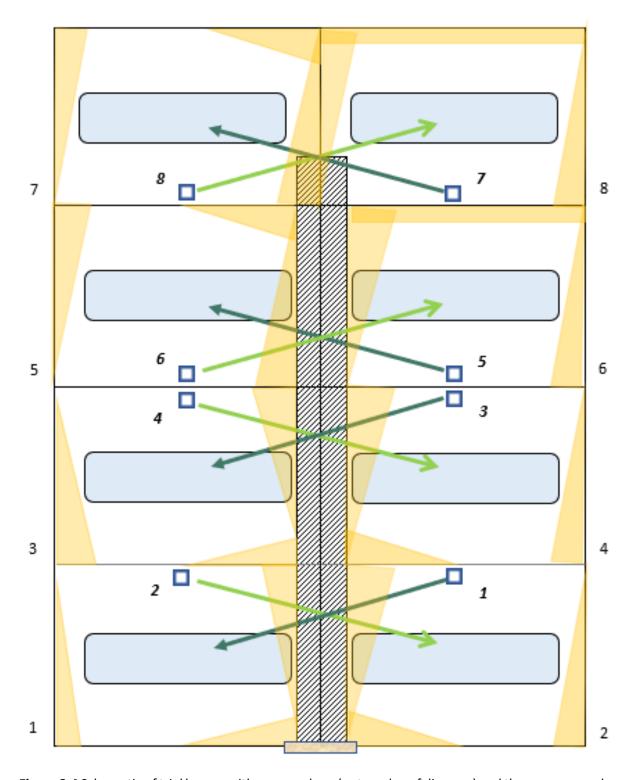


Figure 3.4 Schematic of trial house, with pen numbers (outer edge of diagram) and the camera number (1-8 for each pen in bold next to the cameras - identified by small squares), with arrows demonstrating the direction each camera faced. Shading indicates the approximate portion of the pen area not visible to the cameras (not to scale, just the idea of which areas were not visible).



3.5 Stress

In addition to daily feeding and cleaning, faecal samples were collected twice daily from all pens to ensure the collections were fresh at the time of freezing (Annex F, plate 42). Each sample was weighed (on a kitchen scale) and the weight in grams recorded on both the bag containing the sample itself, and the daily-logs (Annex A) kept on the farm throughout the trial. It should be noted that not every pen produced daily faecal samples, with the lower density pens producing only a fraction compared to the higher density pens. Ziploc bags were used for the faecal collections, and a label on every bag noted the "pen number", "date", "sample weight" and "time" of the collection. The time recording allowed for more than one sample per pen per day, although this was rare. Samples were frozen (-20°C) immediately after collection and delivered monthly (Annex F, plate 43) from the farm to the Endocrine Research Laboratory (ERL) at the Faculty of Veterinary Science, Onderstepoort, Gauteng, South Africa. Faecal samples were transported between the two sites in a cooler box with multiple ice-bricks to ensure minimal defrosting before reaching the laboratory, where the samples were sorted and kept frozen until the processing and analyses could be performed. Owing to time and monetary restrictions, a randomisation was used to select samples for analyses. Of the 1213 samples collected during the trial period, 184 samples were selected for FGM analyses. Stress was analysed using the faecal glucocorticoid metabolite analyses discussed previously. This method of stress analyses was verified for the Nile crocodile by Ganswindt et al. (2014), and similarly utilized in the current study.

A brief overview of faecal sample preparation:

- A. Lyophilisation (freeze-drying).
- B. Pulverisation of freeze-dried samples using hand-held mesh strainers, and a mortar and pestle when needed (Annex F, plate 44).
- C. The weighing and recording of 100-110 mg of faecal powder per sample into storage tubes (occurred monthly with each sample-batch delivery). Each tube was labelled with a code denoting pen, date and time for that sample (Annex F, plate 45).
- D. Steroid extraction using ethanol as a solvent, vortexing and centrifuging the samples for supernatant separation. The final steroid extract was stored frozen (-20°C), until EIA analysis (Annex F, plate 46).

A brief overview of EIA analysis:

- A. Pre-prepared EIA plate defrosting and washing (Goat-Anti Rabbit IgG coated EIA plates).
- B. Addition of standards, quality controls, antibody, biotin labelled-steroid and (appropriately diluted) samples.
- C. All sample additions to the plates were applied in doubles, and the mean values utilized.
- D. Incubations, plate washings, and stopping the reaction (Annex F, plates 47-48).
- E. Reading optical densities using an automatic MTP reader and associated software, with filters at 450 nm and 630 nm.

The sample delivery, processing and analyses (late November - early December 2017) were performed by the author after training received at the Endocrine Research Laboratory at the Faculty of Veterinary Science, Onderstepoort. See Annex E for the stress data recording sheet.

3.6 Skin quality

Experienced handlers assisted in the capture and subduing of the crocodiles whilst skins were being analysed. The crocodiles were scanned for their microchip barcodes, then turned onto their backs and held in place whilst grading occurred. The skins were wiped down with a clean dry towel,



before being graded and photographed (Sony DSLR $\alpha 230$) with their Allflex microchip barcodes alongside for affirmation of which animal was being photographed (Annex F, plate 18).

The grading method for this trial was based on the grading method which was used on the farm at the time of the trial. Since the crocodiles were alive and not yet at a size where they would traditionally be slaughtered and graded, the belly was the only area graded (unlike industry gradings where the full skin is thrown over a light table for grading (Annex F, plate 19)). The belly area is divided into four quadrants, referred to as Q1-Q4. Each quadrant was assessed in terms of the defects present, and the severity of the defects (based off how severe the actual defect was, and the area of the skin that the defect covered). A grade of 1 to 4 was assigned to each skin based on the quadrants assessed (see Annex C). For comparison: a grade 1 animal would have a near perfect skin or a skin that would heal before slaughter size if no more damage were done to it from that point, and a grade 4 would have severe skin defects over multiple quadrants that would likely not heal before slaughter and therefore affect its final grading at slaughter size. For comparison to gradings performed in the industry currently see Figure 3.5 and the associated website. Grades 1-3 would be skins presented for gradings in the market, and grade 4 skins (for the purpose of this trial) would be "cull" animals where the skins are so poor they would likely not be utilized further. Defects identified and included in the skin analyses were: scratches, teeth marks, brownspot, holes, scars, double scaling and abscesses (Annex F, plates 20-28). Some other defects recorded were infection and wrinkles, these defects did not fall into the broad categories named previously and were found rarely but recorded nevertheless. The "infection" defect was recorded as such because the area of skin was severely inflamed (Annex F, plate 20), and the "wrinkle" instances were an odd defect found in a few crocodiles only where fine lines ran parallel to one another over a scale/scales. A single crocodile presented with a selection of spots over two quadrants that did not classify as brownspot or teeth marks, this singular defect was called "Freckles" for lack of a better description. Some types of defects were considered more severe than others; for example: an abscess, especially if gaping open (Annex F, plate 21), was considered the most detrimental to the skins grade, and teeth and scratch defects more detrimental to a skins grade than brownspot for example.

The farm on which the trial occurred keeps their crocodiles in the system until they are at slaughter size, rather than slaughter at a pre-determined age as many other farms do - whether the animals are of an ideal size or not. The farm provided their own workers, with skin grading experience, to assist with the grading and identification of the types of defects found. It was unusual to perform skin gradings on live animals at a smaller size than regular slaughter size; however, perseverance and consistent discussion of the grades allocated at the time of grading ensured everyone involved in the gradings was consistent in this. An image of each skin was captured showing the quadrants so that reflection of the gradings could occur at a later stage.

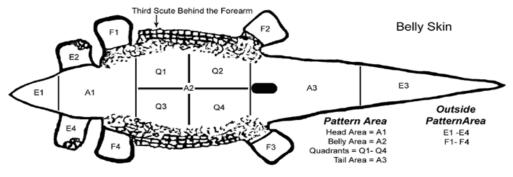


Figure 3.5 Sections of a crocodile skin for skin-grading purposes, sourced from: http://www.rojeleather.com/crocodile-skin-grading/



3.7 Mortalities, illnesses and treatments of crocodiles

Within the first week of the adaption period there was a single mortality, it was deemed early enough in the trial that the crocodile could be replaced immediately. During the trial period 16 crocodiles died giving a 6.13% mortality rate, each death was noted (date, pen, and microchip number), and the number of crocodiles per pen in the data sheets were corrected as per date of recorded deaths. Carcasses were immediately refrigerated and delivered to the Faculty of Veterinary Science as soon as was possible, usually within a day or two of the death, for a complete necropsy. The pathology reports indicated that the deaths could not be attributed to density allocation. The progression of the trial brought with it some health complications, notably Stress septicaemia, which the whole house had to be treated for. Although the 6.13% mortality rate was undesirable, it was not unusually high for crocodiles in this stage of production on the farm. Notably, of this 6.13% mortalities, 5.7% were from high density pens. To summarize the health issues encountered, and how they were treated:

- In mid-May one crocodile (ID 9820004058/48606) in a high-density pen was treated with an oxytetracycline 100mg/ml injection (Engemycin 10%) for a swollen snout and eye. The same animal was treated again for recurrence at the end of May 2017.
- In early June 2017 the same crocodile as above presented with an infected eye and
 was treated with Terra-Cortil Eye/Ear Suspension (hydrocortisone acetate 5 mg,
 oxytetracycline 10mg/ml and polymyxin B sulphate 10 000 iu). Another crocodile (ID
 9820004058/39141) in this high-density pen was treated similarly mid-October 2017.
- A crocodile (ID 9820004058/42293) with a severely twisted and infected tail end was removed from the trial late August 2017 at the farmer's decision, the crocodile died within the week of its removal (Annex F, plate 35).
- In early September 2017 the swabbing of pens near the water-line, and of the eyes of a few randomly selected individual crocodiles from the house presenting with gooey or discoloured eyes occurred. During this sample collection, another crocodile was removed from the trial for a severe missing tail end, and humanely euthanized (Annex F, plate 39).
- There was treatment of all ponds in the trial house in September and October of 2017 with an Ostri-Dox powder (doxycycline hydrochloride 125 mg/g) recommended and supplied to the farm by Prof J.G. Myburgh.



4. DATA ANALYSIS

The effects of density on growth, stress, skin quality and behaviour were analysed using multiple statistical programs. Most of the data for this study was analysed statistically using IBM SPSS Statistics (version 25); in the interests of precision the data was also analysed using SAS (Statistical Analysis System, version 9.4), and when performing cluster analyses the statistical program R (version 3.5.1) was utilized. Multivariate ANOVAs were performed for all data sheets in SPSS. SAS was used to confirm the outcomes of the SPSS outputs for the growth and skin quality data. All data was analysed for the determination of significant differences (P<0.05), and some tendencies were included as well for further discussion of the findings and their potential significance to the current study (P<0.1).

Crocodile growth was analysed multiple times as there was indecision regarding an ideal covariate or weighting-factor to use when performing the ANOVA. Upon reviewing previous studies where growth of crocodilians and fish was assessed, it was clear that the body measures recorded in the current study (total body length, snout vent length, belly width, and weight) had all been used as covariates in previous studies (Brien, 2015; Owerkowicz *et al.*, 2009; Temsiripong *et al.*, 2006; Pinheiro & Lavorenti, 2001). Some studies calculated a "body size measure" which was a compilation of body measures, this compilation measure had also been used before as a covariate in crocodilian studies involving growth assessments (Brandt *et al.*, 2016; Shilton *et al.*, 2014). For the current study Fulton's condition scores, using both pre-trial TBL and pre-trial SVL (calculated with a scaling factor) were calculated for each crocodile and added to the list of covariates tested for. Pre-trial total body length alone was avoided as a covariate due to some of the crocodiles' tail ends being missing (some more substantially than others), and the fact that the animals were selected based upon this measure at the beginning of the trial. After analysing the data in full, these measures were used as weighting factors rather than a covariate.

Corticosterone concentrations were analysed per density group and month of trial using SPSS's univariate GLM analysis. SPSS was used to perform a cluster analysis for this data set due to the categorical nature of the data.

Crocodile skin qualities were analysed for the different density groups in SAS via the Proc Logistic procedure. This aimed to identify significant differences (pre- and post-trial) for the variables: skin grade, number of severely-scored skin quadrants per crocodile, and the defect types in each quadrant per crocodile. The SAS Frequency procedure was incorporated for further comparison and was based off data manipulations where each variable was compared pre- and post-trial and a "skin quality score" assigned. The scores indicated either improvement in each skin quality variable over the trial period, no change over the trial period, or deterioration in quality over the trial period. Frequencies and percentages of these scores were assessed across different density groups and tabulated for easy comparison. Principal component and cluster analyses were performed in SPSS and R respectively for this data set.

The behavioural data was collected in the form of counts of crocodiles seen in each time-lapse image, and their distributions throughout the pen. This data was later edited in the interests of comparability over density groups. Simply put: the number of crocodiles in view would always be greater for the higher density pens, and so the data points where converted into percentages of crocodiles as distributed throughout the pens. Crocodile behaviour was analysed with a multivariate ANOVA in SPSS, and later principal component and cluster analyses were performed in SPSS and R respectively.

All correlation tables were computed with significance levels P<0.05 and P<0.1; the correlations considered influential for the current study are discussed for each section, any results considered obvious or expected were not discussed in-depth. It is important to remember when appraising these sections that correlation is not causation.



Regression analyses were avoided in this study, as the exclusion of certain correlation and linked-factor effects was not desirable. The statistical analyses employed (Bonferroni was widely employed) compensated for unbalanced data encountered.

Cluster analyses were performed to assess potential similarities or dissimilarities across data sets, and to assess the spread of density groups over these clusters via distance functions. Normalisation functions were used prior to these analyses, which were performed using both R and SPSS statistical programs (SPSS was used in cases where clustering had to be performed on categorical variables). Cluster analyses strip away the labels of density, pen or date and look for similarities within the data without these pre-conceptions. After the sorting as described above, densities (for example) could be re-applied to the data in the hope that the clusters formed have a degree of homogeny with the density groupings of crocodiles used in this trial. This could potentially further confirm the effects, or lack thereof, of density on the various measures recorded for the 261 crocodiles in this trial. Regarding the graphs that follow: patterns were used as far as possible to indicate density, this was not possible for all cases (cluster analysis results particularly). For further distinction the following colours were assigned to graphs comparing densities: low (yellow), blue (medium), and high (red).



5. RESULTS AND DISCUSSION

The first month of the trial (mid-May till mid-June) was an adaption period, essential both for the crocodiles and researcher. The house allocated to the trial was newly built, its design was based upon those known to produce well on the farm. As a new and sterile house, it could be viewed as an "idealized' habitat for such a trial. The adaption period allowed the crocodiles assigned to the trial time to adapt to their new housing and pen mates; the workers on the farm to adjust to the new scheduling for the trial; and the setup and testing of hygrometers and cameras by the researcher. Data from this period was recorded and included in the results that follow, one should keep in mind the existence of the adaption period when reviewing these results.

5.1 Climate

In-house ambient temperatures and humidity were recorded hourly during the trial, using the thermo-hygro datalogger (refer to chapter 3.8), to ensure that any potential environmental-causal factors were accounted for (Figures 5.1.1 and 5.1.2). Table 5 summarises the ambient temperature and humidity results for each month of the trial. It should be noted that the in-house temperatures were considerably higher than the external temperatures recorded, humidity differences for the internal and external recordings did not vary as much as temperatures did. Maximum daily in-house temperatures varied from 23.1°C to 70°C, and minimum in-house temperatures ranged from 0°C to 22.9°C. Maximum daily in-house humidity varied from 55.5%RH to 97.5%RH, and minimum in-house humidity ranged from 6.1%RH to 72%RH. When comparing the average in-house temperature and humidity over month of trial it was found that temperature increased between July and September and then plateaued between September and October, and then finally rose again in November. In-house humidity when compared over month declined from July to September, then rose and spiked in October, before finally decreasing rapidly between October and November.

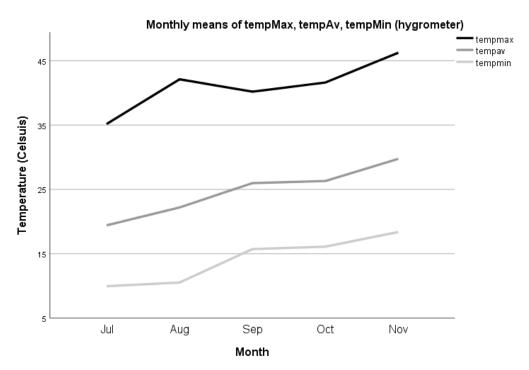


Figure 5.1.1 Mean monthly maximum, average and minimum ambient in-house temperature, recorded by the hygrometer during the trial period.



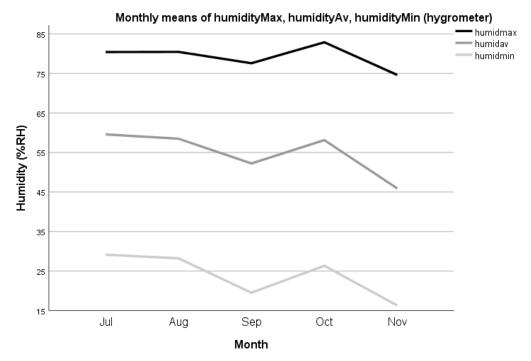


Figure 5.1.2 Mean monthly maximum, average and minimum ambient in-house humidity, recorded by the hygrometer during the trial period.

To supplement the climate data supplied by the hygrometer, temperature and humidity data for the Hartbeespoort area was also included (Figures 5.1.3 and 5.1.4), as supplied from the South African Weather Service (SAWS). Maximum daily external temperatures varied from 12.4°C to 37.6°C, and minimum external temperatures ranged from -2.6°C to 20.5°C. Maximum daily external humidity varied from 46%RH to 98%RH, and minimum external humidity ranged from 6%RH to 74%RH. When comparing the average temperature and humidity for the Hartbeespoort region over month of trial it was found that temperature dipped slightly between May and June, plateauing between June and July, and then increasing from July to September; after which it plateaued till October, and then increased again between October and November. Hartbeespoort humidity when compared over month remained constant from May to June, then declined between June and late July, before plateauing in August, increasing again between September and October, and finally declining between October and November.



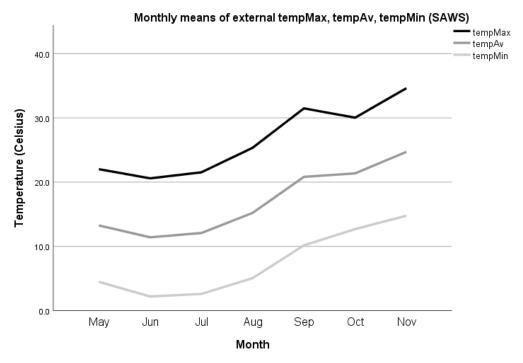


Figure 5.1.3 Mean monthly maximum, average, and minimum temperatures for the Hartbeespoort area supplied by SAWS.

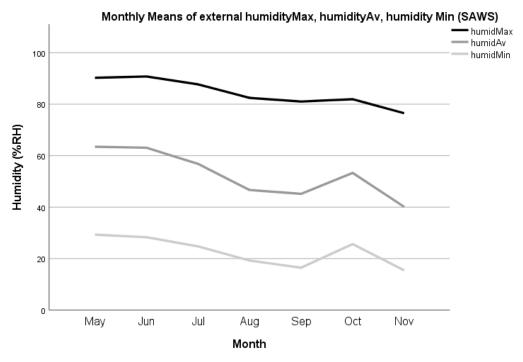


Figure 5.1.4 Mean monthly maximum, average, and minimum humidity for the Hartbeespoort area supplied by SAWS.



Floor and water temperatures were monitored daily for every pen at midday (presumably a warmer time of the day), using the handheld IR thermometer (Chapter 3.8). Table 6 summarises the floor and water temperature results per density for each month of the trial. The minimum and maximum floor temperatures throughout the trial period were 14.9°C and 66.2°C respectively. The minimum and maximum water surface temperatures throughout the trial period were 17.5°C and 67.8°C respectively. Multiple previous studies involving crocodilians have agreed that higher temperatures are beneficial for growth, stress reduction and disease resistance (Moleon et al., 2018; Brien¹ et al., 2014; Shilton et al., 2014; Groffen et al., 2013; Isberg, 2007; Davis, 2001). Midday water surface temperatures were consistently lower than floor temperatures for all months of the trial (Figure 5.1.5), affording the trial crocodiles the opportunity to cool off in the water in need. The water and floor temperatures at midday in the current study however were rather high towards the end of the trial, especially when one considers the optimal temperature range for commercially farmed crocodilians is 24-32°C (Brien, 2015; Shilton, et al., 2014; Tosun, 2013; Bothma & van Rooyen, 2005). Midday floor temperatures exceeded the optimal range from about August onwards. This spike in temperatures, especially from October to November, could have been problematic for the trial crocodiles as although the water temperature was lower than that of the floor temperature, neither the floor nor water temperatures offered any escape from the heat. This may be an area of concern when one considers that summer in Gauteng only begins in November, had the floor and water temperatures remained as high as was recorded toward the end of the current trial throughout the summer months, there would be no escape from the heat for crocodiles housed there.

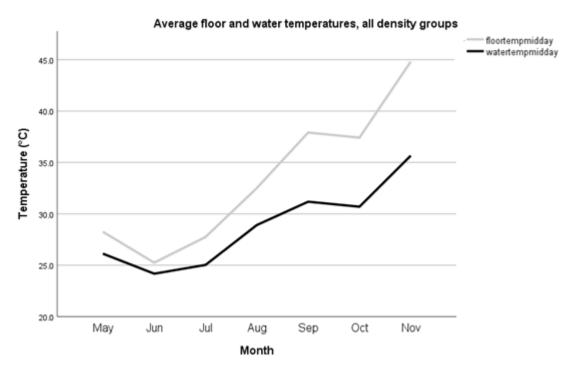


Figure 5.1.5 Mean monthly floor and surface water temperatures in the trial house.

When considering floor temperature (Figure 5.1.6) there were not significant (P<0.05) differences between the densities over month of trial, except September where the high-density pen floor temperatures were significantly lower than those of the low and medium density pens. The explanation for this floor temperature difference exclusively in September remains unknown. Month of trial had a more significant effect on floor temperature changes, with a dip between May and June, and an incline between June and September, plateauing between September and October, and finally



increasing again in November. This pattern mimics that of the monthly temperatures captured by SAWS.

When considering water surface temperature (Figure 5.1.7) there were no significant (P<0.05) differences between the densities during the trial. Once again month had a more significant effect on water temperature changes. Water temperatures dipped between May and June, increased between June and September, plateaued between September and October, and finally increased again in November. This pattern, again mimics that of the monthly temperatures captured by SAWS.

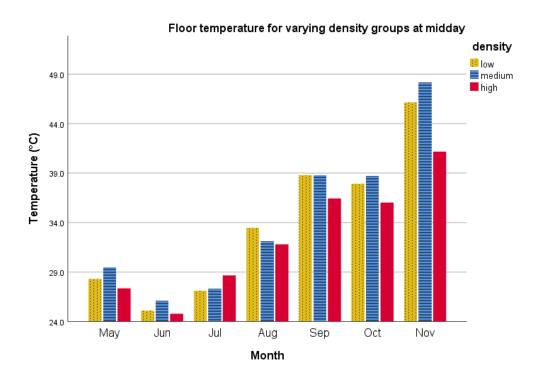


Figure 5.1.6 Mean monthly floor temperature for varying density groups in the trial house.

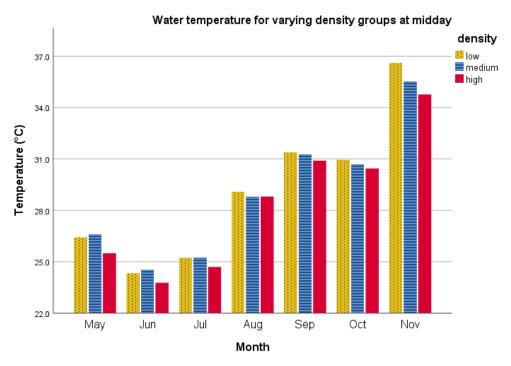


Figure 5.1.7 Mean monthly water temperature for varying density groups in the trial house.



Table 5 External (SAWS) and internal (hygrometer) air temperature and humidity data (x̄ and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa

Data	Month						
	Мау	Jun	lu(Aug	Sep	Oct	Nov
SAWS weather da	SAWS weather data for Hartebeespoort	oort					
z	23	30	31	31	30	31	12
Temp (°C)	13.27 (0.358) a	11.41 (0.222) a	12.08 (0.248) 3	15.21 (0.333) ^b	20.82 (0.389)	21.37 (0.540) ^c	24.72 (0.480) ^d
Humidity (%RH) 63.46 (1.741) ^a	63.46 (1.741) 3	63.08 (1.172) a	56.82 (1.782) 3	46.64 (1.613) ^b	45.16 (1.524) ^b	53.30 (2.673) ab	40.11 (2.496) ^b
In-house Kimo-hygrometer data	grometer data						
z			15	31	30	31	15
Temp (°C)			19.41 (0.183) ₃	22.19 (0.456) ^b	25.97 (0.383) ^c	26.30 (0.517) 5	29.75 (0.481) ^d
Humidity (%RH)	/	/	59.57 (1.240) a	58.49 (1.035) ₃	52.23 (1.187) ab	58.14 (2.204) 3	45.90(2.854) ^b

abcMeans with different superscripts in rows differ significantly (P<0.05)



Table 6 Monthly water and floor temperatures for varying stocking densities (x̄ and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa

Density	Month						
	Мау	June	July	August	September	October	November
Floor temperature							
Low	28.30 (0.541)₃	25.14 (0.280)₃	27.12 (0.301) ₃	33.47 (0.392) ^b	38.79 (0.297) ^c A	39.95 (0.704)	46.14 (0.648) ^d
Medium	29.51 (0.755) ³b	26.11 (0.370) ₃	27.31 (0.340) ₃	32.12 (0.354) ^b	38.79 (0.383) ⁵ A	38.70 (0.889) 5	48.15 (1.049) ط
High	27.36 (0.563) ₃	24.78 (0.368) 3	28.67 (0.707) 3	31.80 (0.295) b	36.44 (0.277) ^{bc} _B	36.02 (0.692)	41.17 (1.560) ^d
Water temperature	ē						
Low	26.42 (0.329) ³b	24.33 (0.246) ^a	25.23 (0.216) 3	29.09 (0.259) b∈	31.38 (0.229) ^{cd}	30.94 (0.407) ^d	36.60 (1.264)*
Medium	26.62 (0435) ³b	24.56 (0.418) 3	25.24 (0.300) ■	28.79 (0.388) b∈	31.28 (0.255) 5	30.70 (0.474) 5	35.53 (0.341) ^d
High	25.50 (0.350) ab	23.77 (0.304) 8	24.70 (0.284) bc	28.81 (0.275) ^{cd}	30.90 (0.182) ^{de}	30.44 (0.403) ⁴	34.77 (0.314)†

abc Means with different superscripts in the same row indicate significant density month-effects (P<0.05) Differences were tested using Bonferroni's multiple range test due to the data set being unbalanced. AB Means with different subscripts in the same column indicate significant density-effects (P<0.05)



Overall, the impression gained after reviewing the results of this section was that the in-house temperatures fluctuated quite extremely, reaching both very cold (at night) and very warm (during the day) temperatures throughout the trial period. The increase in temperatures and decrease in humidity over the course of the trial was typical for the region. When comparing the temperature data collected by the South African Weather Service (SAWS) to the in-house hygrometer data (although recordings only began in July) it became apparent that the ambient temperatures inside of the house, especially towards the end of the trial, were very high. Notably the maximum ambient, floor and water temperatures in August to November rose to above recommendations for optimal production and growth for crocodilians (24-32°C). The crocodiles would likely have been very uncomfortable having to lay on the hot floors towards the end of the trial period, especially since the water bodies would not have offered much relief from the heat considering the temperatures that were reached. The temperature increasing further could have negative effects on production, especially considering in South Africa the summer months only begin in November. In-house temperature monitoring systems with minimum and maximum temperature alerts, more advanced heating (night-time) and cooling (day-time) technologies, or simpler cooling methods such as designated shade-areas within pens could be helpful in alleviating this issue in the future (Manolis & Webb, 2016; Brien, 2015; Brien et al., 2007; Bothma & van Rooyen, 2005; Davis, 2001; www.iucncsg.org [4]). Maintenance of an optimal temperature range in the water bodies of grower pens is just as important as ambient and floor temperature maintenance. The surface water temperatures recorded in the current study indicated that temperatures increased quite dramatically in November. The CSG BMP (Crocodile Specialist Group Best Management Practices) recommends that water bodies not only be deep enough for full submersion of all crocodiles in a pen, but also deep enough to allow "thermal stratification" when ambient temperatures increase above 34°C (Manolis & Webb, 2016). Inability to regulate body temperatures in crocodilians can cause reduced growth and even mortality, follow up research into more efficient temperature monitoring would be a benefit to optimizing crocodilian housing.



5.2 Feed intake

Apart from the first week of the adaption period during the trial, kilograms of feed fed per pen and feed waste per pen was recorded throughout the trial period (mid-May to mid-November 2017); refer back to chapter 3.1 for feeding and waste collection schedule. This allowed the tracking of feed intake per pen, furthermore intake per animal was calculated by dividing the intake per pen by the number of crocodiles in each pen. This is only an approximate value as feed competition and possible dominance behaviours would determine the exact intake of each crocodile.

Feed intake for all densities showed an almost exponential incline over the trial period as the crocodiles grew (Figure 5.2.1). The low and medium density pen crocodiles ate significantly (P<0.05) more feed than those in the high-density pens throughout the trial period, not including the adaption period. Table 7 summarizes the average feed intakes of crocodiles in varying density pens for each month of the trial. The increased feed intake over time could be explained by the crocodiles growing and the increasing ambient temperatures as the trial progressed. The crocodiles may also have been more inclined to eat as the trial progressed, as they became more comfortable and adapted to their new housing.

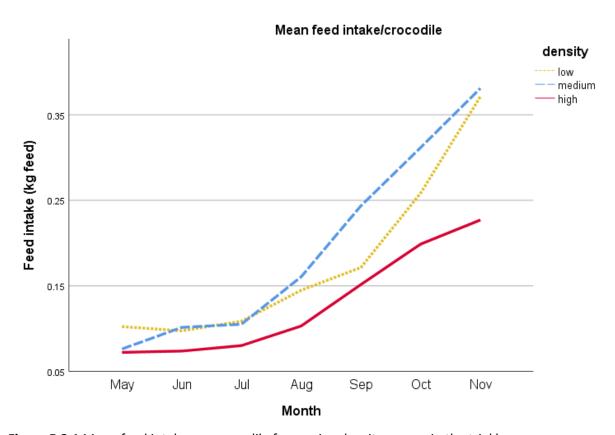


Figure 5.2.1 Mean feed intake per crocodile for varying density groups in the trial house.



Table 7 Monthly feed intake per pen and per crocodile for varying stocking densities (x̄ and S.E) collected May-November 2017 on a commercial crocodile farm in South Africa

Density	Month						
	May	June	July	August	September	October	November
Intake/pen							
Low	1.02 (0.072) a _A	0.97 (0.048) ⁵₄	1.09 (0.045) ³A	$1.45 (0.039) ^{b_A}$	$1.72 (0.066)^{b_A}$	2.58 (0.094) ^c A	3.71 (0.125) d _A
Medium	1.60 (0.149) ³A	$2.13(0.077)^{ab_B}$	2.21 (0.074) b _B	3.37 (0.088) %	5.12 (0.138) d _B	6.55 (0.129) °B	8.00 (0.130) f _B
High	4.55 (0.192) ³B	4.61 (0.170) a _c	4.92 (0.106) ³c	$6.21 (0.111) ^{b_{\rm C}}$	8.87 (0.211) ^c c	11.61 (0.111) d _c	13.20 (0.066) ೀ
Intake/crocodile							
Low	$0.10(0.007)^{a_A}$	0.10 (0.005) a _A	$0.11 (0.005)^{a_A}$	$0.14 (0.004) _{A}$	0.17 (0.007) b _A	0.26 (0.009) ^c A	0.37 (0.012) ^d A
Medium	0.08 (0.007) a _B	$0.10 (0.004)^{ab_A}$	$0.11 (0.004) b_A$	0.16 (0.004) SB	0.24 (0.007) d _B	0.31 (0.006) °s	0.38 (0.006) f _A
High	0.07 (0.003) a _B	0.07 (0.003) a _B	0.08 (0.002) a _B	$0.10(0.002)^{b_c}$	0.15 (0.004) °c	0.20 (0.003) d _c	0.23 (0.004) ^e B

abc Means with different superscripts in the same row indicate significant density month-effects (P<0.05) AB Means with different subscripts in the same column indicate significant density-effects (P<0.05)

Differences were tested using Bonferroni's multiple range test due to the data set being unbalanced



Correlations were computed among all variables in the daily-data analysis, the resulting tables (Tables 8 - 10) can be viewed for the full results of this analysis for the varying density groups. All correlation tables were computed with significance levels P<0.05 and P<0.01.

Table 8 shows the correlations described for the low-density pens, these findings confirm what is seen in the graphs and means-tables for this section. As the date of trial progressed more feed was fed, and less feed waste collected (r=0.830 & -0.505 respectively), supporting the findings of increased intakes per pen and per crocodile as the trial progressed (r=0.820). Temperature and humidity were strongly, negatively correlated (r=-0.816). In-house temperatures, floor temperatures, and water temperatures all correlated positively and strongly with date of trial (r=0.621, r=0.778, r=0.653); whereas humidity showed a high negative correlation with date of trial (r=-0.512). Floor and water temperatures were strongly positively correlated (0.839), but negatively correlated with humidity (r=-0.753 and r=-0.678 respectively). The amount of feed fed showed a high positive correlation (r=0.554) with ambient temperature, and a high negative correlation (r=-0.401) with ambient humidity. The amount of feed waste collected showed converse results, with a moderate to high negative correlation (r=-0.264) with temperature, and a moderate to high positive correlation (r=-0.364) with humidity. Feed intake per pen and per crocodile increased with increasing in-house temperatures (r=0.597) and decreasing humidity (r=-0.518). As ambient temperatures increased so did those of the pen floors (r=0.828) and water bodies (r=0.763).

The results in Table 9 show the correlations for medium-density pens. These results are notably similar to the low-density results (Table 8). As the trial progressed more feed was fed, and less feed waste collected (r= 0.950 & -0.500 respectively), supporting the findings of increased intakes per pen and per crocodile as the trial progressed (r= 0.947). Temperature and humidity were strongly, negatively correlated (r= -0.782). In-house temperatures, floor temperatures, and water temperatures all correlated positively and strongly with date of trial (r= 0.576, r= 0.754, r= 0.662); humidity showed a high negative correlation with date of trial (r= -0.516). Floor and water temperatures were strongly positively correlated with one another (r= 0.824), but negatively correlated with humidity (r= -0.725 and r= -0.672 respectively). The amount of feed fed showed a high positive correlation (r= 0.445) with ambient temperature, and a high negative correlation (r= -0.367) with ambient humidity. The amount of feed waste collected showed converse results, with a moderate to high negative correlation (r= 0.360) with temperature, and no significant correlation with humidity. Feed intake per pen and per crocodile increased with increasing in-house temperatures (r=0.686) and decreasing humidity (r=-0.601). As ambient temperatures increased so did those of the pen floors (r= 0.771) and water bodies (r= 0.726).

An interesting, but low, correlation (r= 0.123) showed that the pen number was correlated to increasing water temperatures for medium density pens. This suggests that the medium density pen closer to the entrance of the house had lower water temperatures during the trial. This finding was not reciprocated in the low-density pens but was similar for high density pens and could potentially be explained by the presence of a White stinkwood tree (*Celtis africana*) on the outside of the trial-house. The tree in question was closest to pen 2 (high density pen); it could also have impacted shading at certain times of the day for pens 1 (medium density pen), 3 (high density pen), and 4 (low density pen). Shading of the pens discussed due by the tree could have been a contributor to the observed temperature difference for the pens in the front of the house. Another explanation for these findings could have been proximity of pens 1 - 4 to the door of the trial house, which was opened daily for entrance into the house during feeding and cleaning times, potentially allowing some of the hot air to escape.

The results in Table 10 show the correlations for high-density pens. As the trial progressed more feed was fed, and less feed waste collected (r= 0.907 & -0.479 respectively), supporting the findings of increased intakes per pen and per crocodile as the trial progressed (r= 0.922 and r= 0.925).



respectively). Temperature and humidity were strongly, negatively correlated (r=-0.821). In-house temperatures, floor temperatures, and water temperatures all correlated positively and strongly with date of trial (r=0.616, r=0.641, r=0.697); humidity showed a high negative correlation with date of trial (r=-0.514). Floor and water temperatures were strongly positively correlated with one another (r=0.761), but negatively correlated with humidity (r=-0.607 and r=-0.706 respectively). The amount of feed fed showed a high positive correlation (r=0.436) with ambient temperature, and a moderate negative correlation (r=-0.284) with ambient humidity. The amount of feed waste collected showed no significant correlations to ambient temperature and humidity in the trial house for high-density pens. Feed intake per pen and per crocodile increased with increasing in-house temperatures (r=0.638 and r=0.640 respectively) and decreasing humidity (r=-0.551 and r=0.556 respectively). As ambient temperatures increased so did those of the pen floors (r=0.677) and water bodies (r=0.805).



Table 8 Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for low stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017

	Pen	Animals	Date	Week	Feed	Feed	Int	Int	F 07h10	F 15h45	Temp	Humidity	FloorT	Water T
					fed	waste	/ben	/croc						
Pen	1	011	000	000	028	052	039	039	.028	.084	100.	.001	013	690'
Animals	011	1	073	075	170**	۵.	д.	q.	а.	а.	083	980.	063	048
Date	000	073	1	. .666.	.830**	505**	.820**	.820**	060.	.139	.621**	512**	.778**	.653**
Week	000	075	666°	1	.829**	508**	.819**	.819**	.085	.139	.621**	513**	**677.	655**
Feed fed	028	170**	.830**	**829	1	۹.	д.	q.	.065	.165	.554**	401**	.734**	.584**
Feed waste	052	q.	505**	508**	q.	1	516**	516**	.094	268	264**	.364**	359**	320**
Int/ pen	-:039	q.	.820**	**618	q.	516**	1	1.000*	.100	820.	**765	518**	.744**	.645**
Int/ croc	039	q.	.820**	**618.	ч.	516**	1.00**	1	001	820	**792.	518**	.744**	.645**
F 07h10	.028	q.	060	.085	.065	.094	.100	.100	1	192	980	046	.050	.032
F 15h45	.084	q	139	139	.165	268	820.	820.	192	1	.022	070	.052	980.
Тетр	100.	083	.621**	.621**	.554**	264**	**765.	**765	980	.022	1	816**	.828**	.763**
Humidity	.001	.036	512**	513**	401**	.364**	518**	518**	046	070	816**	1	753**	678**
Floor T	013	063	877.	**677.	.734**	359**	.744**	.744**	020.	.052	.828**	753**	1	.839**
Water T	690.	048	.653**	.655**	.584**	320**	.645**	.645**	.032	980.	.763**	678**	.839**	1

Correlation is significant at the 0.05 level (2-tailed)

^{**.} Correlation is significant at the 0.01 level (2-tailed)

b. Cannot be computed because at least one of the variables is constant

Key: Int/pen (intake per pen), Int/croc (intake per crocodile), F 07h10 (faecal samples attained at 07h10), F 15h45 (faecal samples attained at 07h10), Floor T (floor temperature), Water T (water temperature)



Table 9 Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for medium stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017

Pen 1 -b ted waste /pen /roc -b		Pen	Animals	Date	Week	Feed	Feed	III	Int	F 07h10	F 15h45	Temp	Humidity	Floor T	Water T
1 b 000 000 000 -042 -023 -023 -061 -012 -014 -013 -013 -014 -013 -014 -012 -013 -014 -012 -014 -012 -014 <th></th> <th></th> <th></th> <th></th> <th></th> <th>fed</th> <th>waste</th> <th>/pen</th> <th>/croc</th> <th></th> <th></th> <th></th> <th></th> <th></th> <th></th>						fed	waste	/pen	/croc						
b cold-a	Pen	1	д.	000	000.	300.	042	023	023	061	012	.014	.001	.055	.123*
000 b 1 999** 950** -500** 947** 947** 058 267* 576** -516** 000 b 999** 1 949** -504** .946** .957 .271 576** -517** 005 b 950** 949** 1 b b .946** .504** .487** .487** .487** .487** .487** .487** .487** .487** .487** .788** .868** .601** .507 .778 .888** .601** .057 .778 .688** .601** .788** .178 .488* .178 .034 .1 .784** .1 .034 .1 .034 .1 .034 .1 .034 .1 .034 .1 .034 .1 .034 .1 .034 .1 .034 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0 <t< th=""><th>Animals</th><th>۹.</th><th>д.</th><th>а,</th><th>۹.</th><th>а,</th><th>۹.</th><th>۵.</th><th>۹.</th><th>۵.</th><th>а.</th><th>Δ,</th><th>а.</th><th>۹.</th><th>۹.</th></t<>	Animals	۹.	д.	а,	۹.	а,	۹.	۵.	۹.	۵.	а.	Δ,	а.	۹.	۹.
000 b 999* 1 949* -504* 946* 946* 057 271* 576* -517* 000 b 950* 949* 1 b b 215* 173 445* -517* -042 b -560* -560* -564* b -497* 1 1000* -351* -486 -560* -023 b -947* -497* 1 1000* 1 -657 178 -661* -024 b -947* -497* 1000* 1 -657 178 -661* -041 b -497* 1000* 1 -657 178 -661* -041 b -486* 178 -184 1 -634 1 -661* -012 -57* -57* -57* -58* -56* -66* -67* -784 1 -784 1 -784 -784 -784 -784 -784 -7	Date	000	q.	1	666	056:	500**	.947**	.947**	850.	.267*	.576**	516**	.754**	.662**
.005 b .95 .9 .	Week	.000	д.	**666.	1	.949**	504**	.946**	.946**	.057	.271*	.576**	517**	.754**	663**
042 b 500** 504** b 1 497** 497** 497** 497** 497** 497** 497** 497** 497** 1.000** 0.57 1.78 6.86** 501** 023 b 947** 1.000** 1 0.57 1.78 6.86** 601** 051 b 947** 1.000** 1 0.57 1.78 6.86** 601** 061 b 947** 957 0.57 1.78 1.78 6.86** 601** 061 b 958* 957 486 1.78 1.78 1 0.34 1 0.34 1 0.34 1.75 771* 014 b 516** 445** 360** 686** 601** 071 175 782** 1 016 b 516** 366** 516** 611** 601** 071 175 784**	Feed fed	.005	я,	**056	.949**	1	я.	д.	۹.	.215*	.173	.445**	367**	**867.	699.
023 b 947** .b 497** 1 1.000** .057 .178 .686** 601** 023 b .947** .946** b 497** 1.000** 1 .057 .178 .686** 601** 061 b .947** .2497* 1.000** 1 .054 1.01 .680** .057 .034 .022 .071 .071 .071 .071 .072 .074 .071 .072 .071 .072 .071 .072 .071 .072 .071 .072	Feed waste	042	д.	500**	504**	q.	1	497**	497**	351*	-:486	360**	.235	396**	343*
023 b .947** .497** 1.000** 1 .057 .178 .686** .660** .601** 061 b .058 .057 .215* .251* .057 .178 .178 .178 .034 1 .034 .175 .071 .071 .178 <	Int/ pen	023	q.	.947**	.946**	q.	497**	1	1.000**	.057	178	.686**	601**	.831**	.672**
061 -b .058 .057 .251* .057 .057 .057 .054 .054 .052 .071 012 012 012 .178 .178 .178 .034 1 .036 .175 .1	Int/ croc	023	ч.	.947**	.946**	q.	497**	1.000**	1	720.	8/1.	.686**	601**	831**	.672**
012 .b .267* .271* .178 .178 .178 .1034 1 .036 .175 .014 .b .576** .445** 360** .686** .686** .022 .036 1 782** .001 .b 516** 367** .235 601** 601** 071 175 782** 1 .055 .b .754** .754** .736** .831** .831** .108 .232* .771** 725** .123* .b .662** .669** 343* .672** .672** .073 .193 .726** .577**	F 07h10	061	q.	.058	.057	.215*	351*	.057	750.	1	034	.022	071	.108	.073
.014 .b .576** .445** 360** .686** .686** .022 .036 1 782** .001 .b 516** 367** .235 601** 601** 071 175 782** 1 .055 .b .754** .754** .798** 396** .831** .831** .108 .232* .771** 725** .123* .b .663** .669** 343* .672** .672** .073 .193 .726** .672**	F 15h45	012	ч.	.267*	.271*	.173	486	.178	.178	034	1	980.	175	.232*	.193
.001 .b 516** 367** .235 601** 601** 071 175 782** 1 .055 .b .754** .754** .798** .396** .831** .831** .108 .232* .771** .725** .123* .b .663** .669** 343* .672** .672** .073 .193 .726** .672**	Temp	.014	ч.	.576**	.576**	.445**	360**	.686**	989	.022	980.	1	782**	.771**	.726**
.055 .b .754** .754** .798** .396** .831** .831** .108 .232* .771**725** .772** .572** .573** .562** .663** .669** .343* .572** .672** .672** .073 .193 .726**672** .672**	Humidity	.001	q.	516**	517**	367**	.235	601**	601**	071	175	782**	1	725**	672**
.123* .h .662** .663** .669**343* .672** .672** .073 .193 .726**672**	Floor T	.055	q.	.754**	.754**	.798**	396**	.831**	.831**	.108	.232*	.771**	725**	1	.824**
	Water T	.123*	ч.	.662**	.663**	**699.	343*	.672**	.672**	.073	.193	.726**	672**	.824**	1

Correlation is significant at the 0.05 level (2-tailed)

Correlation is significant at the 0.01 level (2-tailed)

Key: Int/pen (intake per pen), Int/croc (intake per crocodile), F 07h10 (faecal samples attained at 07h10), F 15h45 (faecal samples attained at 07h10), Floor T (floor temperature), Water T b. Cannot be computed because at least one of the variables is constant (water temperature)



Table 10 Correlations for daily recordings of feed, faecal samples, internal temperatures and humidity for high stocking density pens of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017

		Anim												
	Pen	als	Date	Week	Feed	Feed	lut	lnt	F 07h10	F 15h45	Temp	Humidity	Floor T	Water T
					fed	waste	/pen	/croc						
Pen	1	.548**	000.	000.	850.	.316	:063	022	-:003	.045	004	500:	.025	*760.
Animals	.548**	1	559	558"	427**	479	428"	538**	141"	230"	358**	.318"	318"	299**
Date	000.	559	1	666	200	479**	.922**	.925**	.252**	.213*	.616**	514**	.641**	
Week	000	558**	666	1	906:	479**	.921"	.924"	.248**	.216*	.615"	516"	.642**	869.
Feed fed	850.	427**	200	906.	1	а.	а.	а.	.328"	179	.436**	284**	.617"	879
Feed waste	316	.479	479**	479**	э.	1	603	575"	158	190	088	032	311	205
Int/ pen	.063	428**	.922**	.921"	а.	603	1	166.	.134	.345**	.638**	551"	.623"	.719**
Int/ croc	022	538**	.925"	.924"	л.	575	166.	1	.137	267	.640**	556**	610"	.704**
F 07h10	003	141**	.252"	.248**	.328"	158	.134	.137	1	880.	.118*	110*	.178**	.1961.
F 15h45	.045	230"	.213*	.216*	179	190	.345**	198"	880'	1	:063	048	060:	.195
Temp	004	358**	919.	.615"	.436"	088	859	640**	.118*	.063	1	821"		808.
Humidity	500:	.318"	514"	516"	284"	032	551"	556"	110*	048	821**	1	607	706**
Floor T	.025	318**	.641**	.642**	.617**	311	.623**	.610**	.178**	060.		607	1	.761**
Water T	.097*	299**		869:	879	205	.719**	704	.1961.	.195*	.802	706**	761	1

Correlation is significant at the 0.05 level (2-tailed)

Correlation is significant at the 0.01 level (2-tailed)

Key: Int/pen (intake per pen), Int/croc (intake per crocodile), F 07h10 (faecal samples attained at 07h10), F 15h45 (faecal samples attained at 07h10), Floor T (floor temperature), Water T b. Cannot be computed because at least one of the variables is constant (water temperature)



Overall, the increasing intakes over the course of the trial, and the subsequent increase in faecal outputs, were to be expected with the increase in temperatures. Previous studies have suggested that feed intake and growth are positively correlated (Blessing *et al.*, 2014; Tosun, 2013; Brien *et al.*, 2007; Davis, 2001). The higher intakes in the low and medium density pens seen in the results of this section were interesting (Figure 5.2.1). A possible explanation could be the lower number of crocodiles in those pens competing for feed, yielding lower instances of antagonistic interactions to impede feed intakes. The explanation of lower intakes in the high-density pens could be similar to those of previous studies which have suggested that a dominant crocodile could hinder or discourage pen mates from feeding. Similarly, antagonistic interactions associated with many crocodiles feeding in one pen could discourage feeding of certain individuals, or extended feeding opportunities where crocodiles could return to the feed site unhindered (Brien, 2015; Bothma & Van Rooyen, 2005; Davis, 2001).



5.3 Growth

The following morphometric measures were collected pre and post-trial: total body length (TBL), snout vent length (SVL), belly width (BelW) and weight. Fulton's condition scores were then calculated from these measurements (one using TBL which will hereafter be referred to as Fulton's-T, and another using SVL which will hereafter be referred to as Fulton's-S) (refer to chapter 3.4).

TBL, SVL, weight and Fulton's condition scores all showed increases when comparing pre-and post-trial values (Figures 5.3.1 - 5.3.3, 5.3.5 and 5.3.6). BelW was the only variable that showed a decrease when comparing pre- to post-trial values (Figure 5.3.4). This suggests that as the crocodiles grew in length and weight, their belly widths decreased, yielding longer but narrower crocodiles than when the trial began.

Post-trial weight and the associated weight difference (post-pre), differed significantly between density groups (Table 11). Medium density crocodiles gained significantly (P<0.05) more weight over the course of the trial than low density crocodiles. High density crocodiles gained more weight than low density crocodiles as well, but not significantly (P>0.05) so. Although the crocodiles were randomly assigned to a density group, pre-trial SVL differed significantly between density groups with low density crocodiles exhibiting shorter pre-trial SVLs than high density crocodiles. However, this did not seem to play an important role in their growth as post-trial SVL did not differ between density groups. Notably, both Fulton's scores (Fulton's-T and Fulton's-S) differed significantly (P<0.05) between density groups post-trial. The low-density crocodiles exhibited significantly lower condition scores post-trial than the medium and high-density crocodiles; the medium density crocodiles exhibited similar condition scores post-trial to the high-density crocodiles for both Fulton's-T and Fulton's-S scores (Table 11). This suggests perhaps that the low-density crocodiles may not have been as comfortable in their surroundings yielding loss in body condition.

When considering tendencies toward significance (P<0.1) there were similar findings as above. All weight recordings (pre-/post-/difference) tended to differ, with low density crocodiles exhibiting lower values than high density crocodiles. BelW difference (post - pre) tended to differ, with low density crocodiles exhibiting greater losses in BelW than the medium or high-density crocodiles. Pre-trial Fulton's-T tended to differ between low density crocodiles and those of medium/high density crocodiles, this finding became more significant in the post-trial recordings of Fulton's-T (as discussed above).

The data was further analysed with a multivariate ANOVA using weighting factors, as have been seen in previous studies examining growth in crocodilian and fish species. Multiple variables were contenders when considering the use of a weighting factor, each option assessed will be discussed presently. Interestingly, when the following measures were used as weighting factors (note they were not used simultaneously) there were no significant differences found for any morphometric measures between the density groups: pre-trial weight, pre-trial SVL and pre-trial Fulton's-T. When pre-trial BelW was used as a weighting factor it was found that post-trial weight differed significantly (P<0.05) with density, as was discussed above.



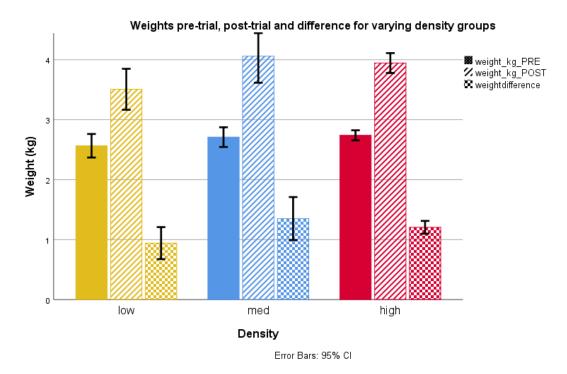


Figure 5.3.1 Mean weight measures (pre, post, and difference) for crocodiles housed at varying densities.

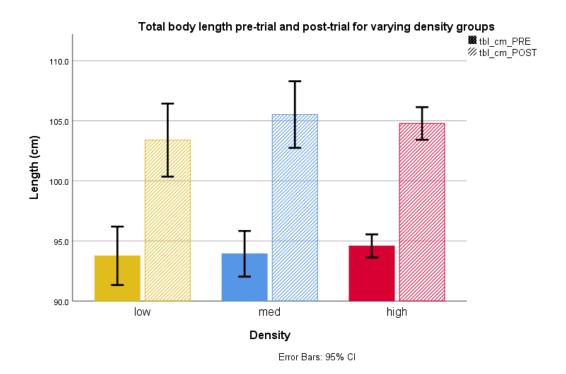


Figure 5.3.2 Pre- and post-trial mean TBL for crocodiles housed at varying densities.



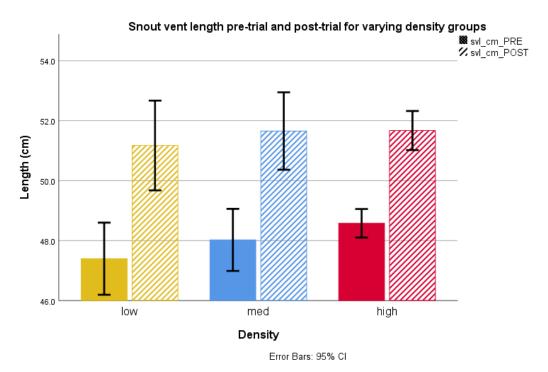


Figure 5.3.3 Pre- and post-trial mean SVL for crocodiles housed at varying densities.

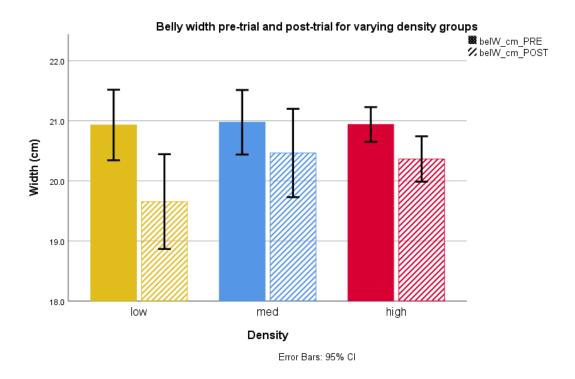


Figure 5.3.4 Pre- and post-trial mean BelW for crocodiles housed at varying densities.



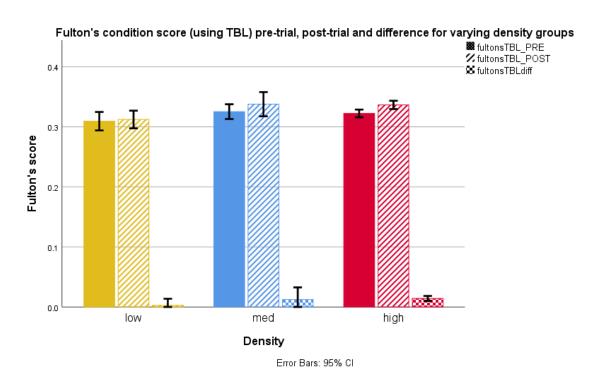


Figure 5.3.5 Mean Fulton's-T (pre, post, and difference) for crocodiles housed at varying densities.

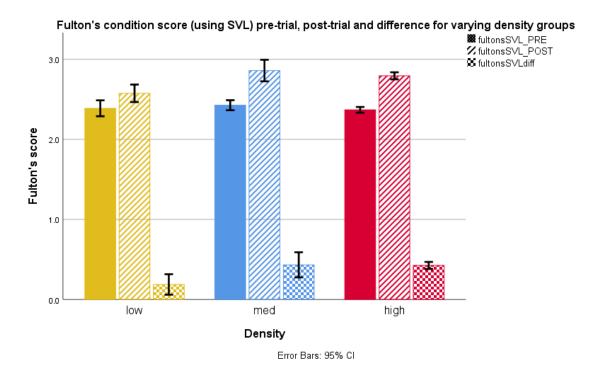


Figure 5.3.6 Mean Fulton's-S (pre, post, and difference) for crocodiles housed at varying densities.



Table 11 The effects of density on growth traits (X and S.E) of grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017

Growth variable	Density					
	z	Low	z	Medium	z	High
Weight Pre-trial (kg)	30	2.55 (0.100) c	42	2.71 (0.084) cd	189	2.74 (0.040) d
Weight Post-trial (kg)	29	3.51 (0.213) a c	42	4.06 (0.177) ^b cd	174	3.95 (0.087) ab d
Weight difference (kg)	29	0.94 (0.149) a c	42	1.35 (0.124) b cd	174	1.21 (0.061) ab d
TBL Pre-trial (cm)	30	93.75 (1.170)	42	93.93 (0.989)	189	94.56 (0.466)
TBL Post-trial (cm)	29	103.40 (1.657)	42	105.52 (1.377)	174	104.78 (0.676)
TBL difference (cm)	29	9.64 (1.008)	42	11.60 (0.838)	174	10.20 (0.412)
SVL Pre-trial (cm)	30	47.35 (0.583) 2	42	48.02 (0.493) ab	189	48.57 (0.232) ^b
SVL Post-trial (cm)	29	51.17 (0.794)	42	51.65 (0.659)	174	51.67 (0.324)
SVL difference (cm)	29	3.78 (0.518)	42	3.63 (0.431)	174	3.09 (0.212)
BeIW Pre-trial (cm)	30	20.90 (0.342)	42	20.98 (0.290)	189	20.99 (0.137)
BeIW Post-trial (cm)	29	19.66 (0.454)	42	20.46 (0.378)	174	20.37 (0.186)
BeIW difference (cm)	29	-1.28 (0.337) _c	42	-0.51 (0.280) d	174	-0.57 (0.138) d
Fultons-T Pre-trial	30	0.308 (0.0079)	42	0.325 (0.0067) d	189	0.323 (0.0031) d
Fultons-T Post-trial	29	0.312 (0.0091) a	42	0.338 (0.0076) b	174	0.337 (0.0037) b
Fultons-T difference	29	0.003 (0.0068)	42	0.012 (0.0057)	174	0.014 (0.0028)
Fultons-S Pre-trial	30	2.38 (0.044)	42	2.43 (0.037)	189	2.37 (0.017)
Fultons-S Post-trial	29	2.58 (0.060) 3	42	2.86 (0.050) ^b	174	2.79 (0.024) ^b
Fultons-S difference	29	0.19 (0.064) ^a	42	0.43 (0.053) b	174	0.43 (0.026) b

ab Means with different superscript letters in same row differ significantly (P<0.05)

 $^{^{\}rm cd}$ Means with different subscript letters in same row tended to differ (P<0.1)



Correlations were computed amongst all growth variables, the resulting tables (Tables 11 - 13) can be viewed for the full results of this analysis for varying densities. All correlation tables were computed with significance levels P<0.05 and P<0.01.

Table 11 shows the correlations for low density group findings. Pre-trial weight for crocodiles stocked at low density was strongly and positively correlated (P<0.05) with all other pre-trial morphometric measures (TBL, SVL, BelW) and both pre-trial Fulton's condition scores. This suggests heavier crocodiles pre-trial were also longer (TBL and SVL), wider (BelW), and in better condition than lighter animals. These heavier pre-trial crocodiles showed strong positive correlations with the post-trial growth measures as well. This suggests the heavier the crocodile was before the trial: the more the crocodile weighed, and the longer and wider it was at the end of the trial. Pre-trial TBL was strongly and positively correlated with pre-trial SVL and BelW for low density crocodiles; similarly, post-trial TBL was strongly and positively correlated with post-trial SVL and BelW. The results indicate that the length measures, TBL and SVL, were strongly positively correlated with BelW, both pre- and post-trial for crocodiles stocked at low density.

Table 12 shows the growth variable correlations for medium density pens. Moderate to strong positive correlations indicate that crocodiles that were heavier at the beginning of the trial were also longer and wider than lighter weight crocodiles at the beginning of the trial for this density group. Crocodiles that started the trial heavier showed strong positive correlations with post trial weights, lengths, widths and both Fulton's condition scores. There was a low positive correlation between pretrial weight and weight difference, indicating that there was a tendency for crocodiles starting the trial heavier to gain more weight during the trial. A high negative correlation (r = -0.335) indicates crocodiles in the medium density groups with longer pre-trial SVL had lower pre-trial Fulton's-S condition scores; this suggests that the longer crocodiles had smaller belly widths, and *vice versa*. Strong positive correlations indicate crocodiles that were longer in length pre-trial, were longer and wider post-trial. BelW pre-trial was highly and positively correlated with BelW and Fulton's condition scores post-trial, and BelW post-trial was highly and positively correlated beginning the trial in better condition than their fellows, maintained better condition scores post-trial.

Table 14 summarises the growth variable correlations for high density pens. As with the low and medium pens, pre-trial weight was strongly positively correlated with all other pre-trial measures of lengths, width and condition scores. Strong positive correlations indicate that heavier crocodiles pre-trial were heavier, longer, wider and in better condition post-trial. Post-trial weight also had strong positive correlations with all pre-trial growth measures and all post-trial measures. TBL pre-trial was positively correlated to pre-trial SVL and BelW, but interestingly negatively correlated to Fulton's-T both pre- (r = -0.373) and post-trial (r = -0.337). This suggests that the longer the crocodile was before the trial, the lower the Fulton's-T scores it attained post-trial.

The correlations discussed showed considerable consistency over the different densities, verifying the reliability of these findings. The results suggest that regardless of density, the larger a crocodile (larger defined in terms of weight, length, and width) was pre-trial the heavier, longer and wider the crocodile was post-trial. This could possibly have been indicative of a degree of FTT in some of the smaller trial crocodiles, as they tended not to grow as efficiently as their larger pen mates.



Table 12 Correlations between growth variables for grower Nile crocodiles stocked at low density at a commercial crocodile farm in South Africa, 2017.

	Weight	Weight	Weight	TBL	TBL	SVL	SVL	BW	BW	Fultons	Fultons	Fultons	Fultons	Fultons	Fultons
	PRE	POST	Diff	PRE	POST	PRE	POST	PRE	POST	T PRE	T POST	T Diff	S PRE	S POST	S Diff
Weight PRE	1	.624**	:063	.748**	.635**	.843**	.510**	.838**	.512**	.443*	.149	-399°	.398	.385	.033
Weight POST	.624**	1	.819**	.425*	.853**	.648**	**628.	.604**	.813**	.377*	.456*	980.	.042	.414	.322
Weight Diff	.063	**618.	1	012	.624**	.209	.749**	.157	.663**	172	.473**	.403*	227	.246	.387
TBL PRE	.748**	.425*	012	1	**869.	.863**	.355	.658**	272.	243	339	105	025	.265	.247
TBL POST	.635**	.853**	.624**	**869.	1	.764**	.810**	.574**	.640**	810.	046	880:-	089	.299	.325
SVL PRE	.843**	.648**	.209	.863**	.764**	1	.582**	.768**	.497**	620	029	127	135	.285	.361
SVL POST	.510**	**678.	.749**	.355	.810**	.582**	1	.541**	.675**	.320	.304	041	039	037	002
BW PRE	.838**	.604**	.157	.658**	.574**	.768**	.541**	1	.449*	.321	.151	229	.213	.237	.048
BW POST	.512**	.813**	.663**	272.	.640**	.497**	.675**	.449*	1	.444	.500**	.050	.101	.461	.316
Fultons T PRE	.443*	.377*	.172	243	.018	620.	.320	.321	.444*	1	.746**	408*	.636"	.227	290
Fultons T POST	.149	.456*	.473**	339	046	029	.304	.151	.500**	.746**	1	.304	302	.369.	.081
Fultons T Diff	399*	980.	.403*	105	088	127	041	229	.050	408*	.304	1	478"	.182	.526"
Fultons S PRE	.398°	.042	227	025	089	135	039	.213	.101	636	.302	478"	1	.252	562"
Fultons S POST	.385	.414	.246	.265	299	.285	037	.237	.461	722.	.369	.182	.252	1	.629
Fultons S Diff	.033	.322	.387°	.247	.325	.361	002	.048	.316	290	180.	.226	562"	659	1

**. Correlation is significant at the 0.01 level (2-tailed).

^{*.} Correlation is significant at the 0.05 level (2-tailed).



Table 13 Correlations between growth variables for grower Nile crocodiles stocked at medium density at a commercial crocodile farm in South Africa, 2017.

	Weight	Weight	Weight	Ē	IBI	INS	75	RW	BW.	Cultons	Eultone	Fulfons	Fultons	Fultons	Fultons
	PRE	POST	Diff	P. B.	POST	PRE	POST	PRE	POST	T PRE	T POST	TDİff	S PRE	S POST	S Diff
Weight PRE	1	.651**	.347*	.808.	.628**	.903**	.710**	608.	.616**	.279	.358*	.188	.093	.359°	.270
Weight POST	.651**	1	.938**	**665.	.740**	629.	.843**	099	.732**	.072	689.	.646**	117	.742"	.682"
Weight Diff	.347*	.938**	1	.371*	.627**	.426**	.716**	.445**	.622**	039	687**	.712**	188	.753"	.719"
TBL PRE	808:	**665.	.371*	1	689	.840**	.704**	.719**	566**	334*	.159	.363*	174	.236	.271
TBL POST	.628**	.740**	.627**	689	1	.566**	.894**	.649**	.759**	091	.044	.100	.107	.262	.181
SVL PRE	**£06.	**679.	.426**	.840**	.566**	1	.674**	.746**	.542**	620.	.439**	.391*	.332,	.421"	.494"
SVL POST	.710**	.843**	.716**	.704**	.894**	.674**	1	.618**	.799**	.013	.308*	.300	670	.292	.238
BW PRE	.809**	099.	.445**	.719**	.649**	.746**	.618**	1	.653**	.135	.313*	.231	.071	.471"	.374*
BW POST	.616**	.732**	.622**	.566**	.759**	.542**	.799**	.653**	1	.078	.321*	.274	.106	.395	.295
Fultons T PRE	.279	.072	039	334*	091	620.	.013	.135	.078	1	.308*	303	.441"	.190	014
Fultons T POST	.358*	.689**	.687**	.159	.044	.439**	.308*	.313*	.321*	.308*	1	.813**	220	.849"	.814"
Fultons T Diff	.188	.646**	.712**	.363*	.100	.391*	.300	.231	.274	303	.813**	1	490"	.734"	.823"
Fultons S PRE	.093	117	188	174	.107	335	.029	.071	.106	.441"	220	490"	1	160	536"
Fultons S POST	.359*	.742"	.753"	.236	.262	.421"	292	.471"	.395"	.190	.849"	.734"	160	1	.919"
Fultons S Diff	.270	682"	.719"	.271	.181	.494"	.238	.374*	.295	014	.814"	.823"	536"	.919"	1

^{**.} Correlation is significant at the 0.01 level (2-tailed).

^{*.} Correlation is significant at the 0.05 level (2-tailed).



Fultons -.402" -.052 201" Sdiff -.021 .378.. .610.. -.031 -.047 393 .899 237 053 .157 11 Table 14 Correlations between growth variables for grower Nile crocodiles stocked at high density at a commercial crocodile farm in South Africa, 2017. Fultons S POST -.002 .216" 443, -.057 149 .072 262 464 .398 .413* .413* .899 .620 521 Fultons -215" S PRE -.238 -.405 324" .255. .119 .413* 295 -.037 .114 .372 499 .160 301 Fultons -.238 TDiff -.019 -207 -.143 -046 -.039 -119 .413* 610 409 .160 172, 361 90 ⊣ Fultons T POST -.337** .377 445 -110 328 808 .378 182 409 620 026 162 257 301 Н Fultons .241" T PRE 271** -.373** 244 -.088 -.207 .499* 808 .398 301 019 171 350 11 Н 241** .711** 533 .810 .772** 328** POST 324 464 *778 .766* 557 784 .172 201 ΒW .491 -119 -.052 .704 .715 .350 .372* .793 .547 .639 .622 .262 .689 257 PRE ΒW Н POST .912 . 915 .772 828 777 114 .072 -021 .709° 803 .689 SVL 171 .162 90 Н -.215" -.002 .448 * PRE .725 .826 .803 .622 -.039 SVL .865 557 019 .764 .026 .157 Н POST 795** .912** .868 .836 -.110 -.046 .730 -.088 .119 .149 .639 .766* .053 764 丽 Н .533 -.373* -.337* -.019 -.037 -.057 -.047 .346 .836 PRE .620 .826 .709 TBL .787 547 IJ Weight 521** :06 .810 .244* .346** .730 .445 ij 448 .160 .393, 521 777 .361 491, П Weight POST .877 .837** .301** :06 .620 .868 :216 .715 .255 .443* 725 .160 377, 237 П Weight .711** .271** .521** 795 -.143 .837 .216 787 .865 828 793* 295 -.031 .182 Fultons S Fultons T **Fultons T Fultons T** Fultons S Fultons S Weight Weight Weight POST POST POST POST SVL POST POST PRE μi Ħ 뙲 SVL PRE BW PRE ΒW TBL

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).



Cluster analysis of the growth data showed that this data could be clustered into two distinct clusters (Figure 5.3.7). "Difference" values were calculated for each variable (Post - Pre) encompassing both the pre- and post-trial measures. The averages for the different cluster groupings were found to be significantly different. Means for each growth measure in these two clusters is displayed in Table 15. Please note there are two columns per cluster, one giving the normalized cluster centres as essential in generating the graphs, and another indicating the means per variable (units specified in the first column) for the data points in the cluster in question. When re-asserting density into the clustered data there were no discernible effects. The densities were semi-equally distributed over the clusters, with no distinct cluster being dominated by any density group (Figure 5.3.8 and Table 16). It is interesting that the data clustered so well, unfortunately for the purposes of this study density was not the causal factor. This analysis confirmed that density did not have the expected effects on growth that were hypothesized, this supports the findings of the previously discussed analyses.

Table 15 Cluster means for growth data.

Growth variables	Cluster 1	Cluster 1 means	Cluster 2	Cluster 2
	(Normalized)		(Normalized)	means
Weight difference (kg)	0.70	1.76	-0.69	0.64
TBL difference (cm)	0.77	14.55	-0.76	6.24
SVL difference (cm)	0.75	5.37	-0.75	1.18
BW difference (cm)	0.54	0.34	-0.54	-1.63

Growth Cluster Plot (colored by cluster)

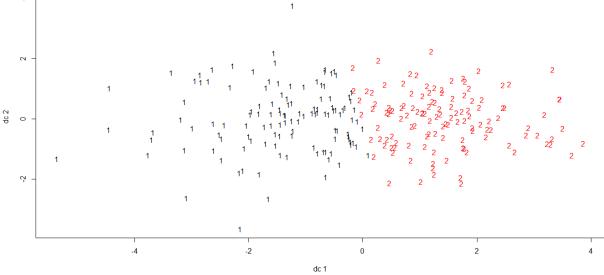


Figure 5.3.7 Growth data clusters. Coloured (cluster 1: black, cluster 2: red) and numbered by cluster.



Growth Cluster Plot (colored by density)

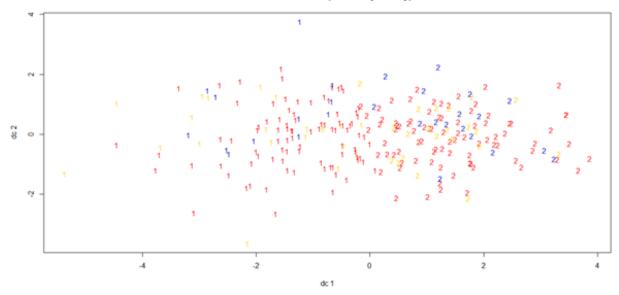


Figure 5.3.8 Growth data clusters. Coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.

Table 16 Frequency table indicating distribution of density groups over clusters for growth data.

Density	Cluster 1	Cluster 2
Low	41.4 %	58.6 %
Medium	50.0 %	50.0 %
High	51.1 %	48.9 %

As can be seen in the frequency table and the graphs coloured by density (low = yellow, blue = medium, red = high), the densities are fairly evenly spread over the clusters (Figures 5.3.8 - 5.3.9). The results of this analysis suggest that density did not have the expected effects on growth that were hypothesized, this could potentially point towards other variables impacting growth that were not measured in this particular study.

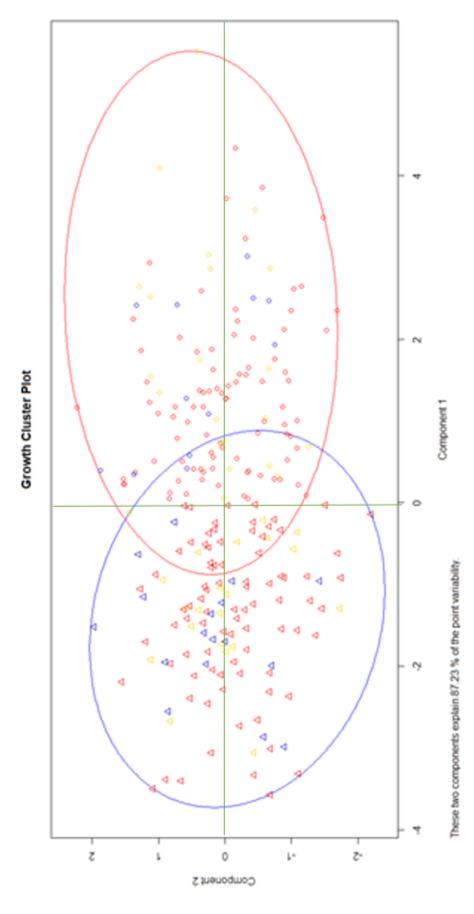


Figure 5.3.9 Growth data clusters. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.



Overall, the findings of this section indicate that density significantly affected growth in terms of weight and body condition scores (Fulton's-T and Fulton's-S). The results indicate that the lowdensity crocodiles did not gain weight as successfully as the medium or high-density crocodiles with the medium density crocodiles outperforming the high- and low-density crocodiles in terms of weight gain. The Fulton's results were similar, low density crocodiles did not gain condition as efficiently as the medium and high-density crocodiles, medium and high-density crocodiles gained condition comparably. Previous studies in crocodilians suggested a negative relationship between stocking density and growth (Brien, 2015; Bothma & Van Rooyen, 2005; Davis, 2001). The findings of the current study however seem to indicate crocodiles in the low-density groupings not growing as efficiently as their medium or high-density counterparts. A possible explanation of this finding could be that low-density crocodiles could have been less active or interactive than those in the medium and high-density groups. Perhaps the reduced need to interact as regularly with pen mates or compete for feed or even be motivated to feed by the feeding behaviours of pen mates could have been the causal factors here. Alternatively, it is possible that the lower number of crocodiles allowed a more stringent hierarchy of sorts, where one or more crocodiles dominated the rest, potentially causing stress and feed intakes that were not as equally balanced as one would hope.

When combining the findings of sections 5.2 and 5.3 the following effect was seen: the high-density crocodiles had the lowest intakes and the medium density crocodiles had the highest for the majority of the trial months, these two density groups also saw greater weight gain and Fultons condition scores post-trial than the low-density crocodiles. In a practical sense it could be reasoned that the high-density group was the most productive; with more crocodiles per farming-area, lower feed intakes and therefore feed costs, and growth similar to that of crocodiles in medium density pens.



5.4 Behaviour

Behaviour of the crocodiles in this study was analysed from a randomised selection of timelapse images captured hourly throughout the trial period.

There were occasions during the recording period where the cameras failed to record their hourly images. This could have been due to battery issues or over-heating of the cameras. Only in one case was it confirmed that the batteries ran out, they were replaced once this was determined and the camera functioned normally thereafter. In other cases, the cameras stopped recording for a few hours and then continued recording thereafter without any human interference. The reason for this is not certain, however a pattern of extremely high temperatures stamped on the images just prior to "camera failure" was noted and hypothesised as the cause thereof. The cameras began recording when temperatures had dropped again. The loss of data was unfortunate, luckily due to the sheer amount of data collected, it was determined that the analyses could be run with the missing values and still yield valuable output.

Piling and contact behaviours were analysed for comparison to skin qualities (which could be affected by excessive piling and the related aggressive interactions when one animal in the pile moved or exited the pile), as well as the faecal stress concentrations (to identify if piling could be considered a stress behaviour). Table 17 summarises the findings, compared over month of trial and densities. When statistically assessing and comparing the results of the time lapse recordings per month of trial it was found that the proportion of crocodiles seen in the water showed an overall decrease from May to November (Figure 5.4.1). The proportion of crocodiles on land increased from June to November for high and low-density pens, whereas the proportion in the medium density pens (showing no discernible pattern as seen for the low or high-density pens) varied throughout the trial period (Figure 5.4.2). The reasons for these findings were likely the increased temperatures as the trial progressed. It has been previously confirmed that crocodilians are poikilothermic and tend to seek heat; studies have shown that concrete pen floors maintain higher temperatures than the ponds in warm climates/environments (as discussed in chapter 3.1). With this in mind refer back to Figure 5.1.5 in section 5.1 where the findings of the current study support this last statement. It stands to reason that a larger proportion of the crocodiles in the current study could possibly have preferred a position on land for poikilothermy reasons. Water surface temperatures (chapter 3.1) towards the end of the trial (November specifically) reached above optimum for farming crocodilians. It is possible that with the water bodies no longer offering a comfortable temperature range, the crocodiles favoured the land area of the pens in the interests of thermoregulation.



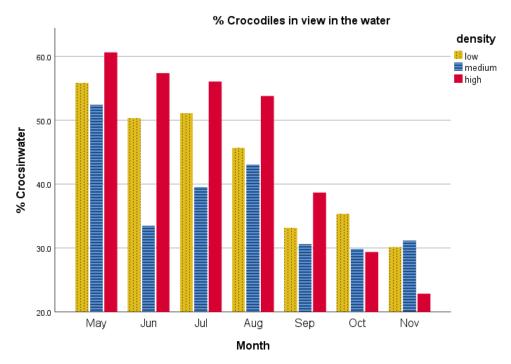


Figure 5.4.1 Mean percentage of crocodiles viewed in the water per month of trial for varying density pens.

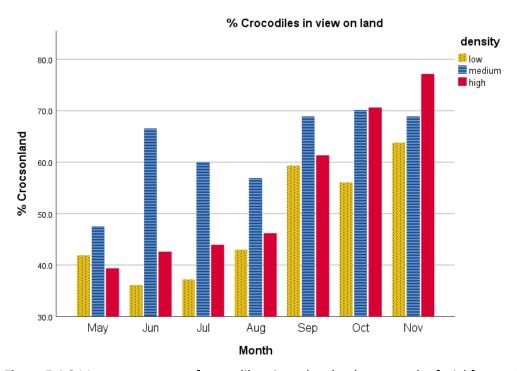


Figure 5.4.2 Mean percentage of crocodiles viewed on land per month of trial for varying density pens.

When considering the proportion of crocodiles in the water that maintained separation from other crocodiles within the pen, the lowest density group maintained higher proportions than the other two density groups, followed by medium and then high-density groups, for the full trial period (Figure 5.4.3). This can easily be explained by the fact that there was more opportunity for the crocodiles stocked at lower densities to remain separate from their pen mates. It stands to reason



that with more space per animal, it is more likely that greater proportions of these crocodiles would be separate from one another. The results for the recordings in the medium and high-density pens support this reasoning, with the medium density pens having significantly (P<0.05) lower proportions of crocodiles in the water separate from their pen mates when compared to the high-density groups, for all months of the trial, except November. Similarly, the high-density pens showed the same trend, with significantly lower proportions of crocodiles separate from their pen mates in the water than that of the medium and low-density pens over all months of the trial.

The results were similar for the proportion of crocodiles on land separate from their pen mates, overall there was a steady increase in this measurement for all density groups, perhaps suggesting that the crocodiles were more inclined to maintain separation from pen mates as the trial continued (Figure 5.4.4). This could potentially be explained by increasing temperatures over the duration of the trial, where contact behaviours in the interests of "heat-seeking" became less necessary. Alternatively, the crocodiles could have become more adapted to their surroundings and pen mates, therefore feeling secure in maintaining separation from pen mates. The low- and medium density pens maintained a greater proportion of crocodiles on land separate from their pen mates, and the high-density pens maintained the smallest proportion of crocodiles on land separate from their pen mates. For the high density group the difference in this proportion was significantly (P<0.05) different from the lower density groups (both low and medium density) for all months of the trial. The medium density pens differed less in this proportion from the low-density group as they did from the higher density group, refer to Table 17. Only the first month of the trial saw significant differences in the proportion of crocodiles separate on land between all density groups. These results could potentially be explained by crocodiles in the high-density pens having less opportunity for separation from pen mates due to space allowances, or perhaps certain more dominant animals-maintained separation from pen mates by forcing the rest of the crocodiles in the same pen to crowd together.

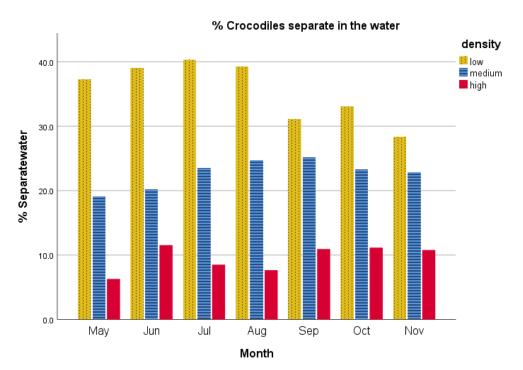


Figure 5.4.3 Mean percentage of crocodiles in the water separate from their pen mates per month of trial for varying density pens.



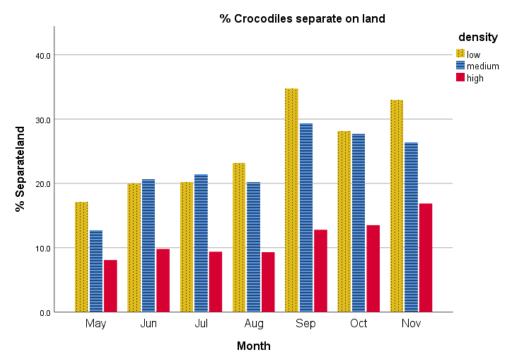


Figure 5.4.4 Mean percentage of crocodiles on land separate from their pen mates per month of trial for varying density pens.

When considering the proportion of crocodiles in the water that were in contact (refer to chapter 3.7 for clarification of contact vs. piling) with their pen mates also in the water, the high-density pens maintained significantly (P<0.05) higher proportions for the trial period, and the low-density pens the lowest (Figure 5.4.5). All density groups differed significantly in their proportions of crocodiles maintaining contact in the water for all months of the trial, except in the months June and November where the proportion of crocodiles in water in contact with pen mates was comparable between the low and medium-density groups. Overall the proportion of crocodiles in contact in the water decreased over the trial period, this is compatible with the findings for crocodiles in view in the water which also showed a decline over the trial period. Simply put: less crocodiles in the water should yield reduced contact activities in the water.

The proportion of crocodiles on land that were in contact with their pen mates increased over the trial period for all densities observed (Figure 5.4.6). Once again this could be related to the previous finding of proportion of crocodiles on land increasing over the trial period, therefore there is more opportunity for contact between pen mates on the land-area of the pens. Low density pens maintained the lowest proportions of crocodiles in contact on land throughout the trial, with medium and high-density groups interchanging between having the greatest proportions of crocodiles in contact on land. The last two months of the trial saw the high-density group differing significantly from the medium density group for this measure. This could possibly be explained by the greater numbers of crocodiles in the higher density groups, finding less space per animal as the temperatures rose and the crocodiles frequented the land area of the pens more regularly.



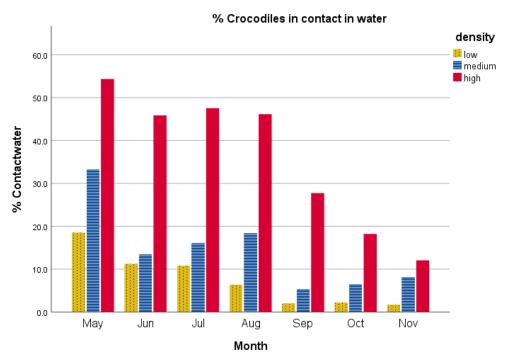


Figure 5.4.5 Mean percentage of crocodiles in the water in contact with their pen mates per month of trial for varying density pens.

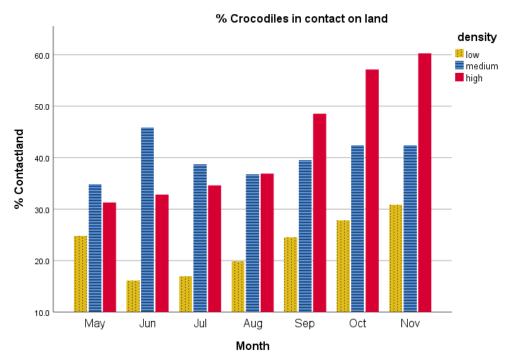


Figure 5.4.6 Mean percentage of crocodiles on land in contact with their pen mates per month of trial for varying density pens.

When considering the proportion of crocodiles in the water that were involved in piling with their pen mates, the high-density crocodiles consistently maintained the highest proportions of piling in the water for the trial period, and the low-density pens the lowest proportions (Figure 5.4.7). For all densities assessed, the trials progression saw a decrease in the proportion of crocodiles piling in



the water. The proportion of piling in water differed significantly (P<0.05) between low and high-density pens for all months of the trial, and medium density groups differed from both low and high-density groups for the months of May, August and September. The remaining months of the trial saw the medium density group differing significantly from the high-density, but not the low-density group.

The proportion of crocodiles on land involved in piling with their pen mates (similarly to the proportions of crocodiles in contact on land) showed an incline over the trial period for high density pens but varied unremarkably over the trial period for low and medium-density pens (Figure 5.4.8). Low and high-density groups differed significantly (P<0.05) from one another consistently over the trial period when considering the proportions of crocodiles piling on land. The medium density groups had significantly higher proportions of piling on land than the low-density groups for all trial months except November, whereas the medium and high-density groups did not significantly differ on a continuous basis. These findings are in line with the space allowances afforded the crocodiles for differing density pens, with higher stocked crocodiles having less opportunity for avoidance of penmates. With less space per crocodile it stands to reason that piling activities would be more severe as the crocodiles attempt to occupy the same spaces within a pen, as the findings confirm.

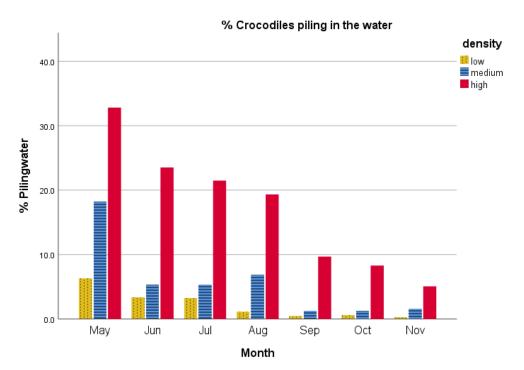


Figure 5.4.7 Mean percentage of crocodiles in the water involved in piling with their pen mates per month of trial for varying density pens.



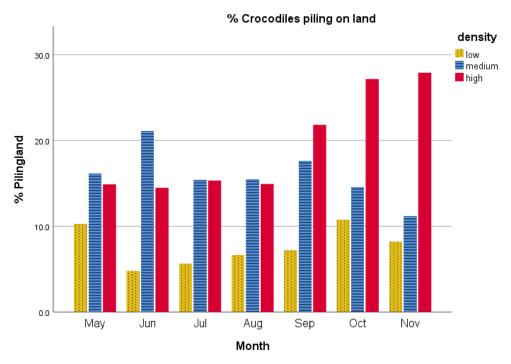


Figure 5.4.8 Mean percentage of crocodiles on land involved in piling with their pen mates per month of trial for varying density pens.

The above findings raise some important questions regarding whether or not the crocodiles in the lower or higher density groups were more comfortable in terms of expressing themselves behaviourally. Piling is often interpreted as a "stress" behaviour in commercial farming situations and can be seen as undesirable in terms of potential for skin damage when such piles disperse. The current study began when questions regarding the viability of commercial single pens were being raised. The ethical concerns surrounding this topic are numerous, and further study will be needed to understand the true implications or benefits of such a housing system. In the current study the low, and to an extent the medium, density crocodiles did not seem to have the same extent of piling as the high-density pens. One could argue that this is an obvious finding given the varied space allowances, however it does pose the question: if the crocodiles in the high-density pens had had the same opportunity for separation from pen mates that their low-density counterparts did, could that have been the more "natural", or at least comfortable, behaviour? With the need to "thrive" becoming more important in current animal welfare regulations, this is a very important question. Refer to chapter 2.14, and the related references, for a reminder of why behaviour is considered a welfare domain.

Temperature effects towards the end of the trial period (September – November 2017) are also a potential reasoning for the behavioural outcomes seen. With water and land temperatures reaching upwards of 30 and 35 °C respectively (Figure 5.1.5), and increasing further as the trial continued, the air (ambient) became the coolest area of the pens. Piling or contact behaviours could potentially have been an active thermoregulatory response, where changing of positions from water to land and varying positions on the land was a means to balance the heat load possibly experienced by the young crocodiles when temperatures rose above what could be considered comfortable.



Table 17 The effect of density on behavioural recordings (X and S.E) in grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017.

Density	Density Month	0					
	May (n=408)	Jun (n=540)	Jul (n=558)	Aug (n=558)	Sep (n=540)	Oct (n=558)	Nov (n=183)
%crocs in view							
Low	54.3 (1.10) aA	36.3 (1.24) b _A	37.4 (1.20) bc _A	$40.0 (1.26)^{bc}$	42.0 (1.27) ^{cd} A	46.0 (1.33) ^d	44.4 (2.00) ^{cd}
Medium	$60.1(1.32)^{3}$	54.0 (1.38) hc _B	53.8 (1.25) bc _B	56.6 (1.35) ab _B	49.4 (1.34) ^{cd} B	44.1 (1.03) ^d	44.9 (1.50) ^d
High	56.6 (0.79) aAB	46.2 (0.83) he _C	49.7 (0.80) ^{cd} c	52.1 (0.86) °c	$48.2 (0.81)^{bd}_{c}$	44.6 (0.72) "	39.8 (1.01)†
%crocs in water							
Low	55.8 (2.15) a _{AB}	50.3 (2.00) b _A	51.2 (1.97) ac _A	45.7 (1.88) bc _A	33.16 (1.57) ^d A	35.3 (1.55) dA	30.1 (2.47) ^d AB
Medium	52.4 (2.30) 3A	33.5 (1.69) bdg	39.6 (1.73) ^{cd} B	43.1 (1.74) ^c A	30.6 (1.52) b _A	29.9 (1.56) b _B	$31.1 (2.81)^{bd}$
High	60.6 (1.81) ^a B	57.4 (1.61) ab _c	56.1 (1.64) ac _A	53.8 (1.49) bcg	38.7 (1.09) ^d B	29.4 (1.14) °B	22.9 (1.73) °B
%crocs on land							
Low	$42.0(2.13)^{a_{AB}}$	36.14 (1.91) ^a A	37.2 (1.89) a	43.0 (1.86) ^a A	59.3 (1.69) b _A	$56.0(1.65)^{b_A}$	63.8 (2.69) b _A
Medium	47.6 (2.30) ^a A	66.5 (1.69) ^{bd} B	$60.1 (1.73)^{cd_B}$	56.9 (1.74) 'B	68.8 (1.54) b _B	$70.13(1.56)^{b_B}$	68.9 (2.81) ^{bd} AB
High	39.4 (1.81) ^a B	$42.6 (1.61)^{ab}_{c}$	44.0 (1.64) ^{ac} c	46.2 (1.49) bc _A	61.3 (1.09) ^d A	70.6 (1.14) °B	77.1 (1.73) °B
%separate water							
Low	37.3 (1.79) ac _A	39.1 (1.79) ab _A	40.3 (1.79) ² A	39.3 (1.73) ab _A	31.1 (1.5) °A	$33.08 (1.48)^{bc_A}$	28.4 (2.35) ^c A
Medium	$19.1 (1.27)^{3}_{8}$	$20.2 (1.25)^{ab}_{B}$	$23.5(1.36)^{ab}_{B}$	24.7 (1.28) ab _B	25.2 (1.35) b _B	23.3 (1.19) ^{ab} s	22.9 (2.04) ab _A
High	6.3 (0.36) ³c	$11.5 (0.67)^{b_c}$	8.5 (0.55) a ^c c	7.7 (0.42) ³c	10.9 (0.49) ^b c	$11.2 (0.44)^{b_c}$	$10.8 (0.54)$ bc B
%separate land							
Low	$17.1 (1.1)^{3}$	20.0 (1.34) ^a A	$20.24 (1.32)^{3}$	$23.2(1.30)^{ab}$	34.8 (1.46) ^c A	28.16 (1.38) bd _A	33.0 (2.63) ^{cd} A
Medium	$12.8 (1.02)^{a_B}$	$20.6(1.32)^{b_A}$	$21.4(1.21)^{b_A}$	$20.2 (1.12)^{b_A}$	29.4 (1.42) ^c A	27.7 (1.37) ^c A	26.4 (2.05) bc _A
High	8.09 (0.42) a _c	9.8 (0.41) 3B	9.4 (0.39) ¹ B	9.3 (0.38) ⁸	12.8 (0.47) b _B	$13.5 (0.50)$ $^{\rm b}_{\rm B}$	16.9 (0.95) 'B

abe Means in rows with different superscripts differ significantly (P<0.05)

AB Means in columns with different subscripts differ significantly (P<0.05)



Table 17 continued... The effect of density on behavioural recordings (X and S.E) in grower Nile crocodiles at a commercial crocodile farm in South Africa, 2017

<u>Density</u>	Month						
	May (n=408)	Jun (n=540)	Jul (n=558)	Aug (n=558)	Sep (n=540)	Oct (n=558)	Nov (n=183)
%contact water							
Low	18.5 (1.40) ^a A	$11.2 (1.08)^{b_{A}}$	$10.8 (1.03)^{b}$	6.4 (0.75) ° _A	2.03 (0.43) ^d A	2.3 (0.44) ^d A	1.7 (0.76) ^{cd} A
Medium	34.9 (2.08) ³ B	$13.4(1.11)^{\mathrm{bc}_{\mathrm{A}}}$	$16.0(1.18)^{c}_{B}$	$18.4 (1.31)^{c_B}$	5.4 (0.70) d _B	6.6 (0.90) d _B	$8.2 (1.70)^{bd}_{B}$
High	$54.3 (1.83)^{3}$	$45.8 (1.58)^{ \mathrm{b}}_{ \mathrm{B}}$	47.5 (1.63) ^b c	$46.1 (1.53)^{ b_{_{\mathrm{C}}}}$	$27.7 (1.11)^{c}$	$18.2~(1.13)^{\rm d}_{\rm C}$	$12.1(1.78)^{d_B}$
%contact land							
Low	$24.8(1.71)^{ac}$	$16.14 (1.26)^{ \mathrm{b}_{ \mathrm{A}}}$	$17.0(1.26)^{b}$	$19.9 (1.26)^{bc}$	24.5 (1.39) ac	27.8 (1.44) ^a A	30.88 (2.74) ^a A
Medium	34.9 (2.08) ³ B	$45.9 (1.61)$ b _B	$38.7 (1.50)^{ab}$	$36.7 (1.62)^{3}_{B}$	39.5 (1.90) ^{ab} _B	$42.4(1.8)^{ab}_{B}$	42.5 (2.98) ab
High	$31.3(1.62)^{\frac{3}{6}}$	$32.8(1.47)^{a_{C}}$	$34.6 (1.54)^{3}$	$36.9 (1.36)^{8}$	$48.5(1.14)^{b_B}$	57.1 (1.09) [€] c	60.3 (1.78) °C
%piling water							
Low	6.3 (0.80) ^a A	$3.4 (0.46)^{b_{A}}$	3.3 (0.47) ^b A	1.1 (0.26) ° A	0.5 (0.17) ^c _A	0.6 (0.23) ^c A	0.29 (0.21) ^c A
Medium	18.2 (1.46) ³ B	5.3 (0.59) bc _A	$5.4 (0.62)^{bc}$	6.8 (0.74) ° _B	1.3 (0.28) dB	1.25 (0.37) ^d A	$1.6 (0.57)^{\text{bd}}_{\text{A}}$
High	32.8 (1.40) ³c	$23.5(1.01)^{b_B}$	$21.5 (0.96)^{bc}_{B}$	19.3 (0.83) °c	9.7 (0.57) ^d c	8.3 (0.65) ⁸	5.1 (0.95) ^d B
%piling land							
Low	$10.3 (1.02)^{ac}$	$4.8 (0.66)^{b_{A}}$	5.6 (0.65) ^b A	6.7 (0.66) b _A	$7.21 (0.69)^{bc}$	$10.77 (0.81)^{\frac{3}{A}}$	$8.2(1.31)^{ab}$
Medium	$16.1 (1.24)^{ab}_{B}$	$21.1 (1.17)^{bc}_{B}$	$15.40 (0.96)$ $^{1}_{B}$	$15.5 (1.06)$ $^{8}_{B}$	$17.7 (1.27)^{ab}_{B}$	$14.6(1.32)^{\frac{3}{8}}$	$11.2 (1.67)^{\frac{3}{A}}$
High	$14.9 (0.90)^{3}$	14.5 (0.78) ³c	15.3 (0.79) ⁸ B	$14.9 (0.68)$ $^{3}_{B}$	21.8 (0.80) b _B	27.2 (0.89) ° _C	27.9 (1.66) ^c B

abe Means in rows with different superscripts differ significantly (P<0.05)

AB Means in columns with different subscripts differ significantly (P<0.05)



Correlations for the behaviour data were computed for each density at the significance levels P<0.05 and P<0.01, and the results displayed in Tables 18 - 20.

The following results were similar across density groups, verifying the reliability of these findings. Correlation values in brackets are in order low, medium, and high density for these results: As the trial progressed the number of crocodiles in view in the water decreased (r=-0.200, r=-0.164, r=-0.348), the number of crocodiles in view on land increased (r=0.197, r=0.162, r=0.348) the number of crocodiles in view on land separate from one another increased (r=0.166, r=0.182, r=0.217), the number of crocodiles in view in the water in contact with one another in the water decreased (r=-0.260, r=-0.286, r=-0.371), the number of crocodiles in view involved in piling in the water decreased (r=-0.195, r=-0.296, r=-0.387).

As in-house temperatures increased, so did the clarity/quality of the water (r= 0.314, r= 0.099, r= 0.104); possibly because as in-house temperatures rose crocodiles frequented the land more, yielding less mess in the water bodies. House temperatures were found to be positively related to the number of crocodiles in view (r= 0.398, r= 0.059, r= 0.235), negatively related to the crocodiles seen in the water (r = -0.432, r = -0.369, r = -0.622) whether in contact with pen mates (r = -0.237, r = -0.327, r= -0.564), separate from pen mates (r= -0.354, r= -0.186, r= -0.148), or involved in piling ((r= -0.156, r= -0.289, r= -0.462). Conversely, temperature was found to be positively related to the crocodiles seen on land (r= 0.579, r= 0.371, r= 0.622), whether separate from pen mates (r= 0.360, r= 0.356, r= 0.270), in contact ((r= 0.422, r= 0.116, r= 0.587). When assessing the correlation between temperatures and piling incidents on land the results also show variation over density (r= 0.319, r= -0.43, r= 0.315), with strong positive correlations for low and high-density groups, and a low negative correlation for medium density. Piling on land was the only set of correlations with temperature that differed between the density groups. It is unclear why the low- and high-density groups were more similar in this regard than the medium density groups, it is possible that there were other factors involved in non-similar outcomes such as this that were not recognised or recorded in the current study.

Water quality was low to moderately positively correlated with crocodiles in view (r= 0.355, r= 0.094, r= 0.338), crocodiles in view on land (r= 0.341, r= 0.077, r= 0.062), and crocodiles in view on land that are in contact with their pen mates (r= 0.294, r= 0.049, r= 0.088). Some land-recordings that are not complementary over all densities include a moderate positive correlation between water quality and crocodiles separate on land for low density pens, and a low negative correlation between water quality and crocodiles separate on land for high density pens. Piling on land showed a low positive correlation to water quality for low- and high-density groups only. Potential justifications for these non-complementary findings are not clear. Water quality showed a low negative correlation when assessing crocodiles in view in the water (r= -0.112, -0.072, r= -0.062), and crocodiles separate in the water (r= -0.141,r= -0.116,r= -0.326). Interestingly only the high-density results showed a low positive correlation between water quality when compared to contact in the water (r= 0.045) and piling in the water (r= 0.074), suggesting that when the water was cleaner, there tended to be more crocodiles in the water involved in contact activities. Another finding that was not consistent over all densities was a low to moderate positive correlation between water quality and piling on land in lowand high-density groups (r= 0.221, r= 0.070). The reasoning behind this finding is unclear, it could be speculated that the higher the density the more animals that were able to contribute towards reduced water quality; high density pens would likely not have had as consistent quality of pen water-body cleanliness as lower density pens, and so when the water was cleanest the crocodiles tended to frequent it more regularly. Another potential explanation is the number of crocodiles in the highdensity pens contributed to lowered water qualities, resulting in murkier water where more crocodiles could submerge themselves and potentially not be counted during the recording of the data, as it is impossible to know if any crocodiles are submerged in the water when it is particularly murky.



When assessing correlations between the land and water activity recordings it should be noted that these variables complement one another, i.e.: if a crocodile is on land it cannot be in the water and *vice versa*, or when a crocodile is separate from its pen mates it cannot be involved in contact or piling behaviours and *vice versa*. The correlation tables confirm this, as can be seen the water and land behavioural recordings (for the most part) were negatively correlated with one another. The proportion of crocodiles separate from their pen mates (for both land and water recordings) was negatively correlated with the proportions of crocodiles in contact or involved in piling (for both land and water recordings). The only exception to this was a low positive correlation between crocodiles separate on land and crocodiles in contact on land for the high-density group only (r= 0.107). This could possibly have been due to there being less space per crocodile in the high-density pens. Conceivably, when a portion of the crocodiles were able to maintain separation from their pen mates, the remaining crocodiles were predisposed to contact activities because of lack of space. Moderate to high correlations dependably showed the higher the proportion of crocodiles viewed in the water; the more crocodiles were involved in separation, contact and piling activities in the water; with less crocodiles engaging in such activities on the land, and *vice versa*.

For all densities, the more crocodiles that were in view, the more crocodiles were seen on land than in the water. Density is a plausible explanation for this finding, but this was not the only factor considered when reviewing this section. High temperatures, combined with crowding (especially in the high-density group), is considered a potential explanation of these findings. The crocodiles could simply have been catering to their own thermoregulatory needs, moving around the pens in such a way to try to cool off. With floor and water temperatures increasing drastically towards the end of the trial, the crocodiles could simply have been attempting to move to a 'cooler' area – the air, hence the increased number of crocodiles occupying the land area of the pens, yielding the increased number of crocodiles seen on land than in the water.



Table 18 Correlations for behavioural recordings in grower Nile crocodiles in low stocking density pens at a commercial crocodile farm in South Africa, 2017.

	Σ	I	>	<u> </u>	A	_	ď	>	%	٧٢	SW	SL	Š	ರ	Α	7
Σ	1	032	986.	000.	376**	.251**	026	002	189**	.191.	075**	.162**	254**	.,960.	188**	.044*
Ŧ	032	1	034*	011	.026	.213**	021	.,260	038*	091**	024	.106**	034*	.018	002	001
>	986	034*	1	000	374**	.254**	033	003	200**	.197**	084**	.166**	260**	.1001.	195**	.041*
<u>~</u>	000	011	000	1	073**	.078**	269	.283**	.152**	022	.032	144**	.257**	.112**	.121**	.045**
4	376**	.026	374**	073**	1	103**	.002	.101	.049**	044*	.003	083**	.,260	.024	.,090	.026
F	.251**	.213**	.254**	.078**	103**	1	.314**	.398**	432**	675.	354**	.360**	237**	.422**	156**	.319**
ď	026	021	033	.269**	.002	.314**	1	.355.	112**	.341**	141**	.167**	.031	.294**	.005	.221**
>	002	**760.	003	.283**	.101.	.398**	.355**	1	164**	.476**	314**	**670.	.246**	.260**	.180**	.437**
*	189**	038*	200**	.152**	.049**	432**	112**	164**	1	772**	.878"	506**	.440**	538**	.279**	357**
7	.191.	091**	.197**	022	044*	**675.	.341**	.476**	772**	1	-:699:-	.,029	356**	.682**	225**	.449**
SW	075**	024	084**	.032	.003	354**	141**	314**	.878	-:699:-	1	430**	044*	474**	048**	312**
S	.162**	.106**	.166**	144**	083**	.360**	.167**	.,620	506**	.,029	430**	1	249**	086**	152**	061**
Š	254**	034*	260**	.257**	.,560	237**	.031	.246**	.440**	356**	044*	249**	1	233**	.671**	159**
ರ	.,960	.018	.100**	.112**	.024	.422**	.294**	.,095	538**	.682**	**474	086**	233**	1	153**	.663**
ĕ	188**	002	195**	.121**	.,090	156**	.005	.180**	.279**	225**	048**	152**	.671**	153**	1	100**
చ	.044*	001	.041*	.045**	.026	.319**	.221**	.437**	357**	.449**	312**	061**	159**	.663**	100**	1

**. Correlation is significant at the 0.01 level (2-tailed).

Correlation is significant at the 0.05 level (2-tailed).

a. Cannot be computed because at least one of the variables is constant.

any other crocodiles), CW (% of crocodiles in the water that are in contact with another/other crocodiles), CM (% of crocodiles), CW (% of crocodiles), CW (% of crocodiles), CM Key: M (month), H (hour), W (week of trial), P (pen), A (number of animals in pen), T (temperature), Q (quality of the water), V (% crocodiles in view), VW (% crocodiles in view that are in the water), VL (% crocodiles in view that are on land), SW (% of crocodiles in the water that are not in contact with any other crocodiles), SL (% of crocodiles on land that are not in contact with of crocodiles in the water that are involved in piling with another/other crocodiles), PL (% of crocodiles on land that are involved in piling with another/other crocodiles).



Table 19 Correlations for behavioural recordings in grower Nile crocodiles in medium stocking density pens at a commercial crocodile farm in South Africa,

	Σ	I	W	Ь	A	L	ď	۸	۸M	NL	SW	SL	CW	CL	PW	PL
Σ	1	030	.986.	000.	в.	.233**	085**	183**	155**	.154**	.063**	.183**	282**	.022	294**	065**
I	030	1	031	016	e .	.214**	038	.049*	094**	.,260	004	.120**	127**	600.	112**	.043*
>	986.	031	1	000	e .	.234**	093**	186**	164**	.162**	.056**	.182**	286**	.031	296**	061**
۵	.000	016	000	1	e .	052*	033	596*-	.300	304**	.410**	.264**	.003	503**	183**	465**
٨	e .	≈.	·*.	≈.	· .	· .	e .	≈.	≈.	· .	≈.	·*.	≈.	· .	· .	æ.
F	.233**	.214**	.234**	052*	e .	1	.,660	.,650.	369**	.371**	186**	.356**	327**	.116**	289**	043*
σ	085**	038	093**	033	₽.	.,660	1	094**	072**	.,077	116**	.040	.018	.049*	029	900.
>	183**	.049*	186**	596:-	г.	.,650	.094**	1	269**	.277**	521**	305**	.153**	.507**	.264**	.435**
*	155**	094**	164**	.300.	e .	369**	072**	269**	1	994**	.,669	380**	989	730**	.441**	445**
٧,	.154**	560	.162**	304**	e .	.371**		.277**	994**	1	694**	.384**	683**	.734**	438**	.448**
SW	.063**	004	950.	.410**	е.	186**	116**	521**	.,669	694**	1	162**	039	586**	112**	360**
SL	.183**	.120**	.182**	.264**	е.	.,956.	.040	305**	380**	.384**	162**	1	365**	346**	262**	340**
Š	282**	127**	286**	.003	e .	327**	.018	.153**	.989	683**	039	365**	1	425**	.730**	256**
Շ	.022	600°	.031	503**	в.	.116**	.049*	.507**	730**	.734**	586**	346**	425**	1	252**	.705**
Α	294**	112**	296**	183**	e .	289**	029	.264**	.441**	438**	112**	262**	.730**	252**	1	146**
7	065**	.043*	061**	465**	е.	043*	900°	.435**	445**	.448**	360**	340**	256**	.705**	146**	1

**. Correlation is significant at the 0.01 level (2-tailed).

Correlation is significant at the 0.05 level (2-tailed).

Cannot be computed because at least one of the variables is constant.

any other crocodiles), CW (% of crocodiles in the water that are in contact with another/other crocodiles), CL (% of crocodiles on land that are in contact with another/other crocodiles), PW (% Key: M (month), H (hour), W (week of trial), P (pen), A (number of animals in pen), T (temperature), Q (quality of the water), V (% crocodiles in view), VW (% crocodiles in view that are in the water), VL (% crocodiles in view that are on land), SW (% of crocodiles in the water that are not in contact with any other crocodiles), SL (%of crocodiles on land that are not in contact with of crocodiles in the water that are involved in piling with another/other crocodiles), PL (% of crocodiles on land that are involved in piling with another/other crocodiles).



Table 20 Correlations for behavioural recordings in grower Nile crocodiles in high stocking density pens at a commercial crocodile farm in South Africa,

	Σ	I	>	_	A	_	ď	>	%	٧,	SW	SL	S	บ	Μ	7
Σ	1	006	986.	000.	553**	.263**	027	156**	339**	.339**	.081**	.,505	360**	.300	376**	.241**
Ŧ	900:-	1	002	018	014	.247**	012	.019	140**	.140**	.015	.174**	143**	.,960.	130**	000.
>	986.	002	1	000.	560**	.270**	032	159**	348**	.348**	.086**	.217**	371**	.307**	387**	.247**
<u>-</u>	000	018	000	1	.545**	091**	.021	256**	.070.	070	.045*	026	922	068**	040*	086**
4	553**	014	560**	.545**	1	204**	.019	.081**	.296**	296**	093**	258**	.322**	238**	.306**	111**
-	.263**	.247**	.270**	091**	204**	1	.104**	.235**	622**	.622**	148**	.270**	564**	.587**	462**	.315**
ď	027	012	032	.021	.019	.104**	1	.338**	062**	.062**	326**	066**	.045*	.088	.074**	070.
>	156**	.019	159**	256**	.081**	.235**	.338**	1	082**	.082**	569**	309**	.103**	.187**	.258**	.1961.
*	339**	140**	348**	070.	.296**	622**	062**	082**	1	-1.000**	.115**	393**	.947**	956	.800	712**
7	.339**	.140**	.348**	070	296**	.622**	062**	.082**	-1.000**	1	115**	.393**	947**	.,956.	800**	.712**
SW	.081**	.015	980	.045*	093**	148**	326**	.,695'-	.115**	115"	1	.166**	210**	177**	236**	154**
SL	.209**	.174**	.217**	026	258**	.270**	066**	.,608:-	393**	.393**	.166**	1	441**	.107**	392**	040*
Š	360**	143**	371**	550:	.322**	564**	.045*	.,201	.947**	947**	210**	441**	1	884**	.864**	651**
ರ	.300	.,960	.307**	068**	238**	.587**	880.	.187	956**	.926.	177**	.107**	884**	1	740**	.784**
δ	376**	130**	387**	040*	.306**	462**	.074**	.,728	.,800	800	236**	392**	.864**	740**	1	550**
చ	.241**	0.000	.247**	086**	111**	.315**	070.	.196**	712**	.712**	154**	040*	651**	.784**	550**	1

 $\ensuremath{^{**}}$. Correlation is significant at the 0.01 level (2-tailed).

Correlation is significant at the 0.05 level (2-tailed).

a. Cannot be computed because at least one of the variables is constant.

any other crocodiles),CW (% of crocodiles in the water that are in contact with another/other crocodiles), CL (% of crocodiles on land that are in contact with another/other crocodiles), PW (% Key: M (month), H (hour), W (week of trial), P (pen), A (number of animals in pen), T (temperature), Q (quality of the water), V (% crocodiles in view), VW (% crocodiles in view that are in the water), VL (% crocodiles in view that are on land), SW (% of crocodiles in the water that are not in contact with any other crocodiles), SL (%of crocodiles on land that are not in contact with of crocodiles in the water that are involved in piling with another/other crocodiles), PL (% of crocodiles on land that are involved in piling with another/other crocodiles).



A principal component analysis of the behavioural data yielded the graph below (Figure 5.4.9), which shows a degree of concord with the correlation results discussed earlier. The graph below suggests an inverse relationship between land and water recordings. The graph suggests the more crocodiles in view the more crocodiles are viewed on land than in the water, this finding concurs with the earlier results of this section. Also suggested is: the more crocodiles on land, and the more crocodiles involved in contact and piling behaviours on land, the less crocodiles in the water involved in these behaviours (and *vice versa*). Similarly, it appears contact/piling behaviours and separation behaviours were inversely related, this concurs with the above findings in the correlation Tables 18-20.

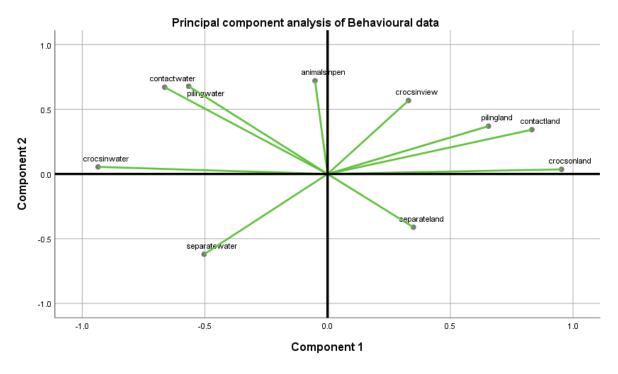


Figure 5.4.9 Principal component analysis of the behavioural data.



Although the cluster analysis of the behavioural data showed that the data could be clustered into three distinct clusters, the clusters formed very atypically. As can be seen in the graphs below (Figures 5.4.10 – 5.4.15) the data clustered into a triangular shape, this was later determined to be a result of the design structure for data collection in this section, where recordings were integrally related to one another. The data was clustered separately in terms of water (Figures 5.4.10 - 5.4.13) and land recordings (Figures 5.4.14 - 5.4.16) in the interest of avoiding the simultaneous analysis of data forming part of a complement. In simple terms: if a crocodile is in the water, it cannot be on land, and *vice versa*. Cluster analyses summarizes a full dataset by pooling all of the data from all three density treatments, it merely demonstrates if there are some clustering effects. These results are not on par with the previous statistical analyses presented in this section. Both water and land clustering results will be reported. The averages for the clusters were found to be significantly different, confirming the viability of sorting the data in this way; with averages listed from first to third cluster for each behavioural measure in Table 21 (water recordings) and Table 23 (land recordings).

Clusters based on water-recordings

Table 21 Cluster means for behavioural data variables recorded for the water-area of pens.

Behavioural variables	Cluster 1 means	Cluster 2 means	Cluster 3 means
Crocodiles in water (%)	85.62	80.90	13.72
Crocodiles separate in water (%)	78.50	12.01	10.00
Crocodiles in contact in water (%)	7.13	68.90	3.72
Crocodiles piling in water (%)	0.74	32.57	1.12

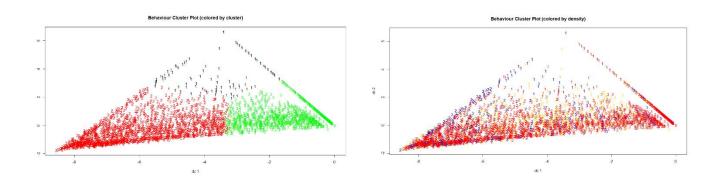


Figure 5.4.10 Behavioural data clusters, clustering performed on water-recordings. Coloured and numbered by cluster (cluster 1: black, cluster 2: red, cluster 3: green).

Figure 5.4.11 Behavioural data clusters, clustering performed on water-recordings. Coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.

When re-asserting density into the data there were no discernible effects over clusters involving water-recordings. The densities were relatively equally distributed over the clusters, with no distinct cluster being dominated by any density group (Table 22). Note when interpreting the "Behaviour Cluster Plot" below that the colours of the points indicate density (low to high: yellow, blue, red) and the shape of the points, as well as the circles around the points indicate the cluster memberships.

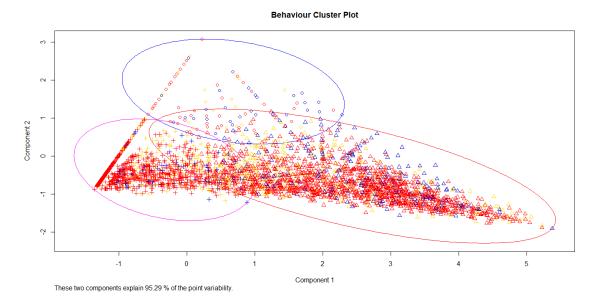


Figure 5.4.12 Behavioural data clusters, clustering performed on water-recordings. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.

Table 22 Frequency table indicating distribution of density over clusters for water-area recordings in the behavioural data.

Density	Cluster 1	Cluster 2	Cluster 3
Low	34.8 %	8.3 %	56.9 %
Medium	17.0 %	18.0 %	65.1 %
High	2.3 %	46.6 %	51.1 %

Clusters based on land-recordings

Table 23 Cluster means for behavioural data variables recorded for the land-area of pens.

Behavioural variables	Cluster 1 means	Cluster 2 means	Cluster 3 means
Crocodiles on land	12.28	79.11	83.96
Crocodiles separate on land	5.91	65.31	14.54
Crocodiles in contact on land	6.37	13.79	69.42
Crocodiles piling on land	2.40	2.30	30.11



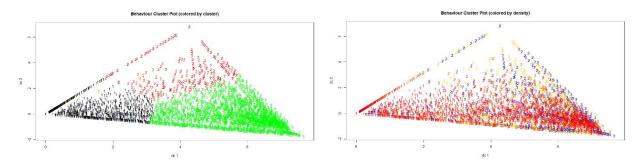


Figure 5.4.13 Behavioural data clusters, clustering performed on land-recordings. Coloured and numbered by cluster (cluster 1: black, cluster 2: red, cluster 3: green).

Figure 5.4.14 Behavioural data clusters, clustering performed on land-recordings. Coloured by density (low: yellow, medium: blue, high: red) and numbered by cluster.

When re-asserting density into the data there were no discernible effects over clusters involving land-recordings. The densities were relatively equally distributed over the clusters, with no distinct cluster being dominated by any density group (Table 24).

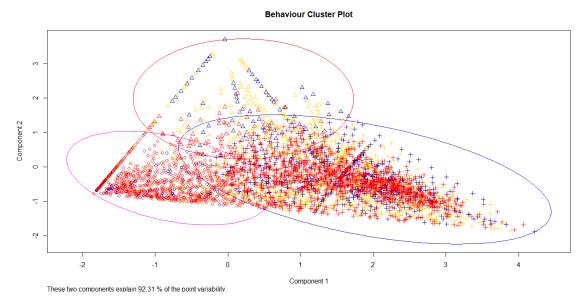


Figure 5.4.15 Behavioural data clusters, clustering performed on land-recordings. Plotted points are coloured by density (low: yellow, medium: blue, high: red) and the shape indicates cluster membership. The circles also indicate clusters.

Table 24 Frequency table indicating distribution of density over clusters for land-area recordings in the behavioural data.

Density	Cluster 1	Cluster 2	Cluster 3
Low	47.2 %	26.0 %	26.7 %
Medium	30.4 %	20.5 %	49.1 %
High	45.4 %	2.7 %	51.8 %



Overall, the findings in this section can be summarised as follows: temperatures increased as the trial progressed, yielding more crocodiles on land than in the water bodies. After reviewing the results of chapter 5.1 this could potentially be explained by the floor and water surface temperatures increasing past the optimal crocodilian-farming temperature range as the trial progressed; in other words, the water bodies ceased acting as an escape from the heat of the ambient temperatures. To combat this issue in the future in-house temperature monitoring and the construction of shaded areas and deeper water bodies could facilitate deceleration of the of warming the water, therefore allowing the crocodiles more opportunity to cool down. Given that the cameras were also likely hindered by the in-house temperatures, temperature monitoring and maintenance could have been beneficial for this aspect as well.

Low density crocodiles maintained the highest proportions of separation activities, which was expected seeing as these crocodiles had more space per animal and therefore more opportunity to separate themselves from pen mates. Contact and piling behaviours showed the opposite result, with the low-density crocodiles maintaining the lowest proportions of these activities, and high-density crocodiles the highest proportions. This finding could once again be explained by the space allowances per crocodile in the varying density groups. The high-density crocodiles showed an increase in piling behaviour on land as the trial progressed, whereas the medium and low-density crocodiles did not show a remarkable increase in this regard. Grouping or gathering of young crocodilians together has been hypothesized as a social or stress related behaviour in both wild and captive crocodilian research (Brien, 2015; Webb et al., 2013; Huchzermeyer, 2003). If piling was socially inclined however it could have been expected that the low and medium density crocodiles in the current study would also have seen an increase in piling as the trial continued and the crocodiles had adapted to their pen mates. With more crocodiles per pen in the high-density pens and the substantial increase in piling seen in this study, it is possible that these animals piled due to stress or potentially as a means of avoiding stress rather than on a social basis. It stands to reason that the high-density crocodiles could therefore have endured more antagonistic interactions, higher frequencies of feed competition, and less opportunity for escape from pen mates. This begs the question: had the high-density crocodiles had the same opportunity for separation from pen mates, would they have been inclined to separate themselves? If this was the case, the question arises whether single pens could be a viable housing option for commercially farmed crocodilians, or whether this would be viewed as an "extreme" production type. More in-depth studies into commercially kept crocodilian behaviours are required before such questions can be fully answered; this will be important to the future of crocodilian farming with quality of life becoming an important production aspect which will apply to both farmers and consumers of crocodilian-products.



5.5 Stress

Faecal corticosterone concentrations were analysed using glucocorticoid metabolite analyses as verified by Ganswindt, 2013 (refer to chapter 3.5).

Although density did not have a significant effect on the corticosterone concentrations during this trial, there were significant (P<0.05) monthly faecal corticosterone fluctuations (Fig 5.5.1). During the adaption period of the trial the faecal corticosterone concentrations for the high-density pens were slightly, but not significantly, higher than those of the medium-density pens. Similarly, the concentrations in the medium-density pens were slightly, but not significantly, higher than those of the low-density pens.

There was a spike in all corticosterone concentrations analysed beginning in late July-August, yielding a peak in concentrations in September-October. The cause(s) behind the peak is unknown, it could possibly have been climatically or metabolically affiliated. According to both the SAWS weather data and the in-house hygrometer temperature measurements, temperature increased over this period. Crocodilians are known to be more active when temperatures rise. It is possible that this increase in activity was accompanied by an increase in aggressive feeding-related behaviours. Another explanation for the spike in corticosterone concentrations near September could be the increase in presence of humans in the trial house at this time, when pond and animal samples were collected when an outbreak of illness was encountered. The sample collections themselves took only a day however, so although this may have contributed to the spike it is unlikely to be the sole cause. Treatments that followed (refer to chapter 3.7) could also have been contributors to the spike in corticosterone during these months of the trial. It is hypothesized that the rise in corticosterone concentrations between August and September (even prior to the sampling that occurred) could have been due to stresses associated with an increase in illness amongst the trial animals, notably the highdensity pens seemed more susceptible to mortality losses than the medium and low-density pens. This might be explained by the space allowances in such pens yielding greater contact and therefore spread of illness among high density crocodiles.

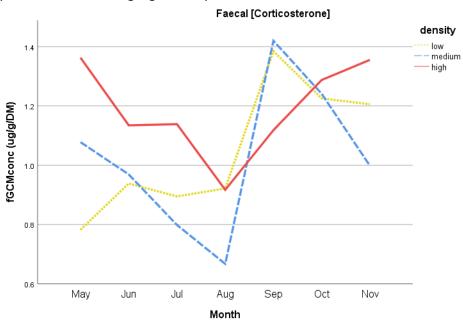


Figure 5.5.1 Mean faecal corticosterone concentrations per month of trial for varying density groups.



Table 25 Correlation table for stress hormone concentrations for grower Nile crocodiles stocked at low, medium, and high densities at a commercial crocodile farm in South Africa, 2017.

	Density	Faecal Corticosterone	Week of trial	Date collected
Faecal	Low	1	.332**	.336**
Corticosterone	Med	1	.999**	.224
	High	1	.999**	.013
Week of	Low	.332**	1	.999**
trial	Med	.999**	1	.219
	High	.999**	1	.011
Date	Low	.336**	.999**	1
collected	Med	.224	.219	1
	High	.013	.011	1

^{**.} Correlation is significant at the 0.01 level (2-tailed)

Table 25 summarises the correlations between faecal corticosterone concentrations in different density groups. It should be noted that the erratic selection of samples makes comparing the concentrations to date of collection a less reliable indicator. Week of trial was positively correlated with faecal corticosterone concentrations for all density groups, with medium and high-density groups had much stronger correlations (r= 0.999) with week of trial than that of the low-density group (r= 0.332).



Cluster analysis of the stress data showed that the data could be clustered into three distinct clusters (Figure 5.5.2). Using a Bonferroni post-hoc analysis: the averages for the different clusters were found to be significantly different; with means listed from first to third cluster for each stress measure in Table 26. When re-asserting density into the data there were no discernible effects. The densities were semi-equally distributed over the clusters, with no distinct cluster being dominated by any specific density group (Table 27).

Table 26 Cluster means for faecal corticosterone concentrations.

	Cluster 1 mean	Cluster 2 mean	Cluster 3 mean
Faecal corticosterone average	2.58	0.71	1.24

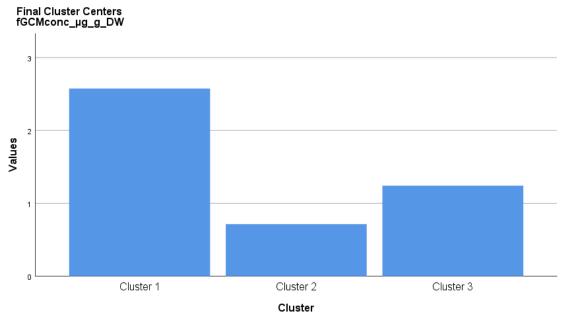


Figure 5.5.2 Stress data cluster analysis.

Table 27 Frequency table indicating distribution of density over clusters for stress data.

Density	Cluster 1	Cluster 2	Cluster 3
Low	5.88 %	50.00 %	44.12 %
Medium	2.17 %	52.17 %	45.66 %
High	8.57 %	37.14 %	54.29 %

The frequency table (Table 27) conveys a similar spread of the density groups over the clusters; this concurs with the previous analyses, suggesting density may not have had a significant effect on stress as hypothesized.



Overall, the findings of this section may suggest that initial (May) stress levels were due to the density placements, the higher the density the higher the corticosterone concentrations. The decrease (May-August) in corticosterone concentrations could have been due to adaption to the new environment/housing. Towards the end of the trial (August to September) temperatures began to rise above optimum, this could explain the increase seen in August – September. The high-density crocodiles seemed less affected until November 2017, when the temperatures were highest. A possible explanation for this could be the combination of extreme temperature stress and a greater number of crocodiles per pen causing a crowding situation. Another potential explanation for the spike in corticosterone concentrations from August – September could be the illness outbreak and the subsequent sampling and treatments that followed.

The various analyses in this section concur that faecal corticosterone concentrations did not vary significantly (P<0.05) between density groups. This is interesting given the extremely high proportions of piling activities seen in the high-density pens, which increased as the trial progressed. This suggests that even when high densities are employed, and rates of piling increase over time, the faecal corticosterone levels do not differ significantly from low or medium density-stocked crocodiles. When referring back to the concluding remarks of chapter 5.4 this could potentially mean that piling, in the context of the current study, is not the best indicator of stress. It is also possible that the range of densities tested in the current study was simply not extreme enough to elicit a severe stress response. Perhaps the piling increase seen could be interpreted, for the purposes of the current study, as a behaviour imposed (not to be overlooked with quality of life becoming more important to consumers) upon high-density crocodiles by a lack of space.



5.6 Skin quality

Ten skin defects were identified amongst the crocodile skins analysed in this trial (abscesses, brownspot, double scaling, freckles, hole, infection, scratch, teeth, wrinkles, and yellowed scars). Refer back to chapter 3.6 for defect descriptions. Of these defects' scratches, teeth marks and brownspot were common occurrences on the farm. Some other defects such as abscesses, double scaling, holes, infection and old/yellowing scars were less common, but easily recognised by the farm workers with experience grading skins; whereas some defects were unusual and rare amongst the trial crocodiles. The experienced farm workers assisting in the grading process did not see these unusual defects frequently, and so unsure of what to classify them as, they were named according to what they resembled (wrinkles and freckles). These rarer defects occurred in only a handful of crocodiles but were included in the analyses nonetheless as the experienced farm workers agreed they would be a detriment to the skins grade once the crocodiles reached slaughter size and their skins would be graded for the market.

Scratches as a defect was the most commonly encountered defect in this trial, followed by teeth marks and brownspot. The prevalence of both teeth marks and brownspot seemed to decrease over the trial period, the defect named holes becomes more prevalent in the post-trial skin analyses. The defect known as "yellowed scarring" became more prevalent post-trial, perhaps indicating that there was opportunity for healing of severe defects as the trial progressed. Drawing conclusions on the less frequently encountered defects would be inexpedient owing to the very low frequencies at which they were encountered; these less-common defects were therefore grouped into a defect category called "other" for the purposes of the analyses that followed.

Each crocodile skin was graded before the trial began and at the end of the trial period. The types of defects, their locations on the skin and their severity were recorded. The skins were graded on a scale of Grade 1 (excellent quality skin) till Grade 4 (poorest quality skins). Tables 27 and 28 summarise the findings in the form of frequencies for the varying density groups, these results were based on output of the GLM Procedure in SAS. No significant (P<0.05) differences between densities were found. However, partial significance (P<0.1), also referred to as tendencies, was included and indicated in the tables; also yielding few significant differences.

The scores 1-3 seen in Tables 27 and 28, called "skin quality" scores, were developed as a comparison of the pre- and post-trial skin analyses, aiming to quantify the changes in skin quality encountered over the trial period. A score of 1 indicates a decline in quality for the skin variable in question once the trial was completed, a score of 2 indicates no change over the course of the trial, and a score of 3 indicates that there was improvement in quality over the trial period. These scores were calculated by comparing pre- and post-trial recordings for the overall grade of the skins, how many quadrants were severe, and the severity of each individual quadrant. Table 29 delves further into the types of defects found; these were compiled by a comparison of pre- and post-trial recordings similarly to the variables in Table 28 and compared by belly skin quadrants. Early analyses showed three defects appearing substantially more often than the rest (scratches, teeth marks, and brownspot), and so for compilation of the frequency tables: the less-common defects were grouped together into a defect category called "other".

As can be seen in Table 28, there were much greater percentages of scores 2 and 3 when comparing skin grades over varying densities. The number of quadrants severe, and severity of each quadrant, showed similar results with scores of 1 (decline in quality) occupying the lowest frequencies. The significance column summarises the findings of the four skin-quadrants assessed, only quadrant 3 had results indicating a tendency toward significant differences (P<0.1) between densities. Overall Table 28 shows a fair comparability over densities, in every case tabulated the score of 2 (indicating no change in quality over the course of the trial) dominated with the highest percentages, followed

by score 3 (improvement in quality), and finally score 1 (decline in quality). It was hypothesised that higher density pens may have endured more antagonistic reactions, therefore reducing skin qualities of these crocodiles. This did not hold true for grade of skin, where (Table 28) high densities had skin quality scores 1-3 falling between those of low and medium densities. Once again it must be noted that although not significant (P<0.05), low density pens fared slightly better as can be seen by the higher frequency of 3rd skin quality scores than the other density groups. This last statement holds true for the other skin quality variables tabulated in Table 28 as well. Crocodiles housed at higher densities did not have remarkably poorer skin qualities than those of the lower and medium density groups. Low density crocodiles had higher (notably however not significant at the level P<0.05) score 3 frequencies than medium and high-density crocodiles when the total number of severe quadrants and the individual quadrant severities were assessed. Medium and high-density animals consistently (but not significantly) saw higher frequencies of score 1 (decline in quality) for each quadrant of the skin assessed, when compared to low-density skin quadrants. As mentioned previously, the lowdensity crocodiles had higher (but not significantly so for quadrants 1, 2 and 4) frequencies of score 3 (improvement in quality) than the medium and high-density crocodiles. Table 28 suggests density was not a factor of importance when skin quality; in terms of grade of skin, number of quadrants severe, and each quadrants severity; was concerned. The frequencies of scores 2 and 3 indicate that the majority (frequencies ranging from 80-90%) of the trial-crocodile skins either did not show a change in quality over the 6-month period of the trial, or yielded improvement in the quality of skins. Grouping the crocodiles into high density pens did not have the effect of lowering skin qualities to the extent expected.

Table 29 shows the effect of stocking density on specific skin defects encountered during the trial, assessed across the four skin quadrants graded for the purposes of defining skin quality. As stated previously, the three dominating defects are scratches, teeth marks and brownspot. Defects not falling into these categories were grouped into the defect type "other" for the purposes of the analysis (results seen in Table 29), to allow more balanced comparisons. Skin quality scores 1-3 were used once again to form this frequency table.

Although scratches were the most common type of defect encountered, no significant differences were found when comparing the prevalence of this defect over the four skin quadrants for the varying density groups. As Table 29 makes clear, a high frequency of crocodiles showed no change in skin quality score for scratches over the trial period, and very small percentages showed improved quality of skin where scratches were concerned. Scratches did not seem to have a good rate of healing and often spanned over many scales and quadrants.

Teeth marks as a defect showed low frequency for score 1 (decline in quality); once again the majority of crocodiles saw no change over the trial period for teeth defect prevalence. There was a higher frequency in score 3 (improved quality) for teeth marks when compared to scratch defects. This could be the result of teeth mark defects tending to be smaller in size than scratch marks, and perhaps this defect type healed at a faster rate because of this. Alternatively, it could also indicate that the crocodiles adapted to their surroundings and pen mates as the trial progressed, leading to lower instances of biting. Quadrant four was the only quadrant were a tendency toward significance (P<0.1) was seen, showing the low-density groups differing from the medium and higher density groups slightly, with a greater frequency of score 3 (quality improvement) attainment. This does not resonate as a significant finding considering P>0.05, and this finding was not reciprocated in the other quadrants for this defect.

Brownspot, similarly to the teeth marks defect, showed minimal (0 - 1.15%) frequency for score 1 (decline in quality). The majority (65.52 - 88.10%) of crocodiles saw no change over the trial period of brownspot defect prevalence, and the remaining crocodiles (11.9 - 26.44%) had scores of 3, indicating improvement in quality of brownspot prevalence over the trial period. Quadrant four was



the only quadrant were a tendency toward significance (P<0.1) was seen, the low-density group tending to differ from the medium and higher density groups slightly, with a greater frequency of score 3 attainment. It is interesting that quadrant four showed this tendency to differ in both the teeth marks defect and brownspot defect; however, definitive conclusions cannot be drawn from this.

The defect grouping of "other" included the defects: abscess, double scaling, hole, freckles, wrinkles, infection, and yellowed scaring. These defects were not as regularly encountered, and some were so minimal they did not occur in every density group. Grouping these defects together was in the best interest of the frequency analysis. A high proportion of these defects showed no change over the trial period (89.08 – 100%). Skin quality scores of 1 were infrequent (0 – 8.62%), and scores of 3 even more so (0 - 3.45%). No significant differences were found between density groups for this defect category.



Table 28 Frequency table showing the effect of stocking density on skin quality of grower Nile crocodiles at a commercial crocodile farm, 2017.

Skin quality variable	Density		Skin quality score		Significance
		1: Declined	2: No change	3: Improved	
Grade of skin	Low	13.79	41.38	44.83	NS
	Med	11.90	57.14	30.95	NS
	High	12.07	53.45	34.48	NS
Number of severe quadrants	Low	10.34	44.83	44.83	NS
	Med	11.90	57.14	30.95	NS
	High	12.64	52.87	34.48	NS
Quadrant 1 severity	Low	10.34	58.62	31.03	NS
	Med	16.67	57.14	26.19	NS
	High	14.37	57.47	28.16	NS
Quadrant 2 severity	Low	17.24	55.17	27.59	NS
	Med	11.90	66.67	21.43	NS
	High	19.54	59.20	21.26	NS
Quadrant 3 severity	Low	10.34	55.17	34.48	а
	Med	23.81	54.76	21.43	Д
	High	13.22	62.64	24.14	Д
Quadrant 4 severity	Low	13.79	58.62	27.59	NS
	Med	16.67	61.90	21.43	NS
	High	14.37	65.52	20.11	NS

ab superscripts in the significance column within a single variable indicate differences with a tendency towards significance (P<0.1), NS: not significant.



Table 29 Frequency table showing the effect of stocking density on skin defects in grower Nile crocodiles at a commercial crocodile farm, 2017.

Defect	Quadrant	Density	S	kin quality scor	·e	Significance
			1:	2:	3:	
Coratch	1	Low	Declined	No change 82.76	Improved 3.45	NS
Scratch	1	Low	13.79	82.76	3.45	INS
	1	Med	14.29	83.33	2.38	NS
	1	High	16.09	80.46	3.45	NS
	2	Low	17.24	79.1	3.45	NS
	2	Med	7.14	85.71	7.14	NS
	2	High	12.64	81.61	5.75	NS
	3	Low	10.34	86.21	3.45	NS
	3	Med	9.52	83.33	7.14	NS
	3	High	16.67	76.44	6.90	NS
	4	Low	13.79	79.31	6.90	NS
	4	Med	2.38	95.24	2.38	NS
	4	High	12.07	79.31	8.62	NS
			1:	2:	3:	Significance
			Declined	No change	Improved	
Teeth	1	Low	-	65.52	34.48	NS
	1	Med	-	78.57	21.43	NS
	1	High	2.30	66.67	31.03	NS
	2	Low	-	68.97	31.03	NS
	2	Med	2.38	78.57	19.05	NS
	2	High	1.15	75.29	23.56	NS
	3	Low	-	65.52	34.48	NS
	3	Med	-	73.81	26.19	NS
	3	High	6.90	61.49	31.61	NS
	4	Low	-	62.07	37.93	а
	4	Med	2.38	78.57	19.05	b
	4	High	5.75	69.54	24.71	b

ab superscripts in the significance column within a quadrant indicate differences with a tendency towards significance (P<0.1), NS: not significant



Table 29 continued... Frequency table showing the effect of stocking density on skin defects in grower Nile crocodiles at a commercial crocodile farm, 2017.

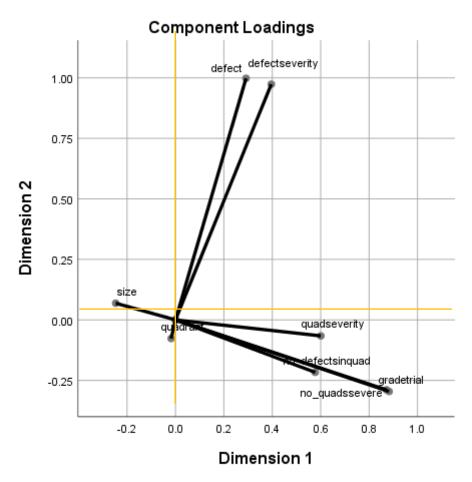
Defect	Quadrant	Density	S	kin quality sco	re	Significance
			1: Declined	2: No change	3: Improved	
Brownspot	1	Low	-	86.21	13.79	NS
	1	Med	-	78.57	21.43	NS
	1	High	1.15	75.29	23.56	NS
	2	Low	-	79.31	20.69	NS
	2	Med	-	76.19	23.81	NS
	2	High	0.57	74.14	25.29	NS
	3	Low	-	82.76	17.24	NS
	3	Med	-	76.19	23.81	NS
	3	High	-	82.18	17.82	NS
	4	Low	-	65.52	34.48	а
	4	Med	-	88.10	11.90	b
	4	High	-	73.56	26.44	b
			1:	2:	3:	Significance
Other	1	Low	Declined -	No change 100.00	Improved -	NS
	1	Med	-	100.00	-	NS
	1	High	4.60	94.25	1.15	NS
	2	Low	6.90	89.66	3.45	NS
	2	Med	-	100.00	-	NS
	2	High	6.90	92.53	0.57	NS
	3	Low	6.90	93.10	-	NS
	3	Med	-	97.62	2.38	NS
	3	High	8.62	89.08	2.30	NS
	4	Low	3.45	93.10	3.45	NS
	4	Med	7.14	92.86	-	NS
	4	High	4.02	95.40	0.57	NS

^{ab} superscripts in the significance column within a quadrant indicate differences with a tendency towards significance (P<0.1), NS: not significant



A principle component analysis of the skin data seems to indicate that the smaller the size of the crocodile, the greater the defect severity (Figure 5.6.1). Perhaps this could be explained by smaller crocodiles having smaller belly widths (a very important factor when determining the value of a skin), conceivably defects might cover a greater area of the belly skin due to this fact. Another relationship with size of crocodile that is suggested by this output is a negative relationship with grade of skin, this proposes that the smaller the crocodile, the higher its skin grade (reminder: the lower the skin grade the better the quality of the skin); and *vice versa*. To offer a potential explanation: the larger crocodiles could have been more able to fend off their pen mates during antagonistic interactions than smaller crocodiles. These smaller crocodiles could potentially have been targeted more frequently in aggressive interactions, as they could have been seen as an easier target than their larger counterparts.

A weak, negative relationship between quadrant number and quadrant severity is also suggested (Figure 5.6.1), refer to Figure 3.5 in materials and methods for a reminder of the layout of the skin quadrants. If this were to be believed, it suggests that the left hand-side of the crocodiles' belly-skins were more severely affected in terms of the volume of defects than that of the right-hand side of the belly. This seems to be comparable with the relationship suggested between quadrant number and defect severity, which is suggestive of the lower numbered quadrants (once again the left-hand side of the crocodile) having more severe defects than the higher numbered quadrants (right hand side of the crocodile).



Variable Principal Normalization.

Figure 5.6.1 Principal component analysis of the behavioural data.

Cluster analysis of the skin data showed that the data could be clustered into three distinct clusters (Figure 5.6.2). The averages for the different cluster groupings were found to be significantly different. Means for each skin measure in the three clusters is displayed in Table 30. Please note there are two columns per cluster: one giving the normalized cluster centres which are essential in generating the graphs and another indicating the means per variable (maximum ranges of the scores per variable are specified in the "skin variable" column) for the data points in the cluster in question. Reminder: skin quality scores are denoted 1-3, indicating: decline in quality, no change in quality and improved quality, respectively. When re-asserting density into the clustered data there were no discernible effects (Table 31).

Table 30 Cluster means for skins data.

Skin variable	Cluster 1 (N)	Cluster 1 means	Cluster 2 (N)	Cluster 2 means	Cluster 3 (N))	Cluster 3 means
Skin grade pre-trial (grades 1-4)	1.40	3.20	-0.54	1.93	-0.34	2.06
Skin grade post-trial (grades 1-4)	0.35	2.17	0.28	2.13	-1.86	1.00
Quadrants severe pre- trial (quads 0-4)	1.35	2.40	-0.53	0.93	-0.33	1.09
Quadrants severe post-trial (quads 0-4)	0.34	1.17	0.27	1.13	-1.79	0.06
Skin quality score (1-3)	0.97	2.86	-0.67	1.79	1.01	2.88

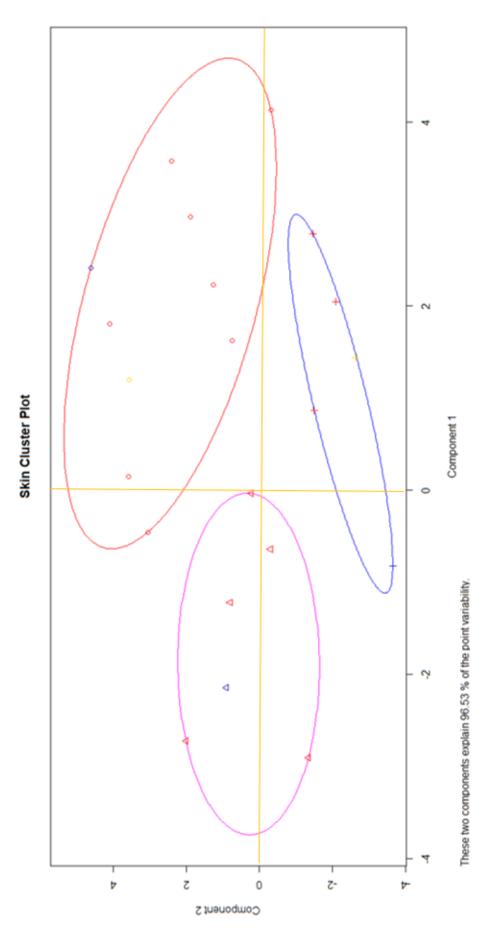
^{*(}N) indicates cluster means when the data is normalized, and "quads" is shorthand for quadrant.

It is important to note in the case of the cluster plot (Figure 5.6.2): the recordings are either in the form of scores (skin grade and skin quality score), or in the case of number of quadrants affected (which can range only from 0 to 4): a numeric value with a very small range of values that would have recurred multiple times throughout the data set. Due to these facts, the points on Figure 5.6.2 cannot be trusted as there are multiple points laying over one another and only the "top" point situated on each location plotted is presented in the plot. The plot is included to show that the data clustered extremely efficiently (as can be seen by the clusters not overlapping one another). The findings confirm, as can be seen in the frequency table (Table 31), that density is not the causal factor of these differences within the data. Density did not have the expected effects on skin quality that were hypothesized for this study.

Table 31 Frequency table indicating distribution of density over clusters for skin data.

Density	Cluster 1	Cluster 2	Cluster 3
Low	31.0 %	48.3 %	20.7 %
Medium	23.8 %	64.3 %	11.9 %
High	26.4 %	60.3 %	13.2 %

As can be seen in the frequency table (Table 31) and the points on the graph coloured by density (low = yellow, blue = medium, red = high) (Figure 5.6.2), the densities are comparably spread over the clusters. The results of this analysis confirmed that density did not have the expected effects on skin quality that were hypothesized, this supports the findings of the previously discussed analyses.



density: yellow, medium density: blue, high density: red), shape of the points plotted indicates cluster membership (cluster 1: triangles, cluster 2: circles, Figure 5.6.2 Skin data clusters. Plotted points have both a shape and a colour; for clarification: points are coloured according to the density group (low cluster 3:plus-signs). The shape of the plotted points is not always easy to discern, and so each cluster group is also encircled on this figure.



Overall, the findings of this section suggest that density did not yield the significant (P<0.05) differences in skin quality that were hypothesized. Some inconsistent tendencies pointed toward the low-density crocodiles having marginally better skin qualities, however due a lack of significance in the statistical analyses this assumption could not be reliably made. The current study hypothesized that higher stress levels might yield higher piling activities, which would in turn reduce skin qualities in the high-density crocodiles. As stated previously this seems not to be the case, as skin qualities did not differ between density groups, and neither did faecal corticosterone concentrations. Once again it can be assumed that if the range of densities tested in the current study was more extreme these results might differ; as in previous crocodilian studies which suggested negative relationships between stocking density and skin quality (Brien, 2015; Bothma & Van Rooyen, 2005; Davis, 2001).

A principal component analysis suggested smaller crocodiles having greater defect severities and higher (poorer) skin grades. It also suggested the left-hand side of the crocodile skins showed higher proportions of skin defects, and more severe defects than that of the right-hand side of the skins. The reasoning behind this left-hand trend is unknown; as for the smaller crocodiles having more severe skin issues, it is possible these smaller crocodiles were targeted more frequently in antagonistic interactions than their larger counterparts.



6. CONCLUSIONS

The results of this study suggest that the current farming practises employ an acceptable range of densities for farming of grower Nile crocodiles. Of the densities assessed in this particular study, there was no definitive "ideal" density that maximised growth and skin qualities, whilst minimizing stress endured. The current study assessed what seemed to be obvious factors for quantification of the effects of stocking density on commercial crocodile production. However, when considering the results, it is clear there were possible factors of importance external to the analysis. The temperature spike toward the end of the trial, and the sampling and treatment when illness presented are important factors to consider when reviewing the results of this study.

Feed intake per crocodile (chapter 5.2) was analysed for the duration of the trial, feed intake increased over the trial period. This was likely due to the increasing temperatures, growth of the crocodiles over the trial period, and possibly indicated the adaption of the crocodiles to their new surroundings and pen mates over time. The findings also indicate that the crocodiles in the higher density pens consumed less feed per crocodile than the low and medium density-stocked crocodiles. This lower intake did not radically affect the growth of the high-density crocodiles during the growth phase under investigation. It is hypothesized that the higher density crocodiles may have exhibited more competitive behaviours during feeding times, yielding reduced intakes by certain individuals in these pens, as suggested in previous studies.

Some significant (P<0.05) differences were observed in the growth assessment (chapter 5.3). Although TBL, SVL and BelW did not differ significantly between density groups, weight and Fulton's condition scores did. The absence of significant differences in the morphometric measures of TBL, SVL and BelW between crocodiles housed at varying densities in the current study was surprising. Crocodiles in the low-density pens experienced six-times the space allowances of crocodiles in the high-density pens for the full trial period but did not grow drastically better or worse than their high-density counterparts. This is potentially indicative of the morphometric measures employed not serving as sensitive enough indicators by which the effects of stocking density should be quantified (the findings of the current study indicate that behaviour or skin quality may have been more important indicators for this). Low-density crocodiles did not fare as well as their higher-density counterparts in terms of weight gain and maintenance of condition (Fulton's). Medium density crocodiles exhibited the greatest weight gain over the course of the trial; and high and medium density crocodiles exhibited significantly higher Fulton's condition scores than low density crocodiles. Notably the measure most important to skin production (BelW) did not differ significantly between the densities tested. However, BelW did tend to differ (P<0.1), suggesting the medium and high-density crocodiles lost marginally less BelW over the course of the trial than low density crocodiles. These findings suggest that the lowest density crocodiles did not yield growth as efficient as the other densities tested. This finding is in opposition to the findings in previous studies which suggested growth and stocking density to be negatively related (Brien, 2015; Brien et al., 2007; Bothma & Van Rooyen, 2005; Davis, 2001). Poletta et al. (2008) conducted a study with broad snouted caimans housed at varying densities and found that growth at low and medium densities was superior to that of the high-density group. Elsey² et al. (1990) studied juvenile American alligators and found that high density-stocked alligators had inhibited growth, and elevated plasma corticosterone concentrations. Overall, the impression gained from the growth results in this study was that the medium density pen crocodiles grew the best, with the low-density crocodiles bringing up the rear.

The results of the behavioural recordings (chapter 5.4) yielded significant differences between the densities tested in the current study. As the trial progressed the crocodiles were less



inclined to spend time in the water-bodies of the pens, and more likely to be viewed on the land. This finding is likely due to the increasing temperatures in the trial house over the course of the trial; possibly more specifically the water surface temperature increases, yielding water bodies that no longer acted as an area in which the crocodiles could cool down. This increase of crocodiles occupying the land-area of the pens likely yielded the increases in contact and piling behaviours seen on land in the high-density pens as the trial progressed; and the decrease of these activities observed in the water-bodies of all density pens. As discussed in chapter 5.4 the lack of an increase in piling in the low and medium density pens as the trial progressed raises the questions of whether the high-density crocodiles would have favoured separation over piling activities had they been afforded the space, and if this were the case: could single pens be considered as an acceptable form of commercial crocodilian housing?

The outcome hypothesized for higher density pens resulting in greater stress hormone concentrations (chapter 5.5) was disproved in the findings of the current study; rather: month of trial had significant (P<0.05) effects on corticosterone concentrations. Faecal corticosterone concentrations showed an overall increase as the trial progressed, this increase was likely due to one or a combination of the following factors: temperatures increasing as the trial progressed, the spread of illness between the trial crocodiles, sampling and treatment procedures that occurred when this illness was noticed (hypothesized to have contributed to the appreciable spike between August and September). Previous studies have not always agreed on the effects of density on stress levels, it is quite possible that the densities tested in the current trial were simply not broad enough to elicit significantly different stress responses. A study by Isberg & Shilton (2013) found no difference in plasma corticosterone levels of individually and communally housed saltwater crocodiles. An older study (Elsey¹ et al., 1990) found that higher-stocked adult American alligators had higher plasma corticosterone concentrations than lower stocked alligators, whose corticosterone levels were comparable to wild American Alligator populations.

The current study hypothesized that higher density pens would result in poorer skin qualities (chapter 5.6), however the results indicate that skin quality did not differ between density groups. Although certain tendencies were observed, significant statistical differences in the skin quality measures were not found. It is interesting that the skin qualities seen in the higher density groups, which yielded the greatest proportion of piling activities, did not differ significantly when compared with the lower density groups. This was an early assumption, which was a cause of concern to the owner due to possible adverse effects associated with high stocking densities. Previously studies have agreed that poor housing, pen design, and immoderate stocking densities cause downgrading of skins due to the increased potential for antagonistic interactions (Mpofu *et al.*, 2015; Isberg *et al.*, 2003); this was not the case in the current study. It is possible that had higher densities than were tested in the present study been utilized (which were not included for ethical reasons), skin qualities, growth or stress levels may have been more severely impacted.

Overall, the outcomes of the current study seem to point towards medium-high densities yielding more productive animals. However, more in-depth analyses are required before commercially kept crocodilian behaviours, which will likely vary with production stage, can be better understood. For future reference: quantifications of the management system; hatchling lineages; previous housing situations; and sounds and vibrations caused by external factors such as generators, activity in adjacent pens/houses, or barking dogs could potentially be considered as factors important to the outcomes of studies such as this one.



7. CRITICAL EVALUATION AND RECOMMENDATIONS

- If this study were repeated in any way, a greater number of repetitions per density tested would yield more accurate statistical findings.
- Assessing different age categories for comparison and a more comprehensive understanding
 of crocodilians in farming situations across different stages of production is suggested for
 future studies.
- A trial encompassing a larger proportion of the growth cycle would also have been beneficial for the recording of production responses and is recommended for future studies.
- Repetition of such a study on farms with different management systems is recommended, as the findings of the current study will not apply to all commercial farms.
- Temperatures in the trial house (especially towards the end of the trial) were higher than
 desired, if this study were to be replicated a more concise temperature control regime would
 have to be implemented for surety that the results are not swayed by extreme temperature
 imbalances.
- This study assessed obvious skin defects and subsequent skin quality gradings on live crocodiles. Although the defects identified would undoubtedly form part of a commercial grading, there might also be less superficial defects in the skins that a light table would expose. In the interests of maximising the accuracy of the skin quality comparisons, it is suggested to lengthen the trial period to include slaughter and commercial skin gradings, as are usually performed on light tables.
- To avoid unnecessary stress and interference with the stress recordings collected, there were no during-trial measurements for growth and skin data in the current study. The results of the stress data indicated a possible stress reaction to human presence for the purposes of sample collections when the trial crocodiles presented with illness. It would be helpful to incorporate growth and skin assessments more frequently in future studies, but only if this could be achieved without severely stressing the crocodiles.
- As mentioned previously, behaviour of commercially farmed crocodilians is poorly understood. Further studies into behaviour of commercially kept crocodilians would be enlightening, and informative to farmers wishing to maximise production and contentment of their stock.
- Individual identification for stress and behavioural data collections was not possible for the current study. Following the progress of certain individuals could be informative for all the production variables analysed, if this were possible in future studies.
- Gender determination was one aspect of the current study that was anticipated as important, but unfortunately was not possible as the crocodiles were too small when selected for the trial. It is recommended that research into more accessible gender identification methods for young/small crocodilians be conducted and incorporated into future studies.
- If manageable at the study site it would be beneficial to track nest/hatchling lineages for incorporation into future studies. Familial comparisons in commercial crocodilian farming could potentially be the next step in maximising production, as has been seen for multiple other domestic-farmed species.
- The commercial farm on which this study occurred now has over 200 microchipped crocodiles, it would be beneficial to make use of this for further studies. Some ideas in this line of thought:
 - Liaise with Allflex (on a genetics-based study) who already have the tissue samples from these crocodiles.



 Design a study testing single pens in the finishing phase in which feed intake, growth and meat quality, propensity for skin healing, stress levels and/or behaviour could be assessed and compared to communally kept crocodilians in the same stage of production.



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[6] http://www.iucncsg.org/pages/The-Crocodilian-Body.html (accessed February 26, 2017)

[7] http://www.iucncsg.org/pages/CCBM-Section-6.html (accessed February 15, 2018)

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ANNEXURES

Annex A: daily log recording sheet, one supplied for each pen, renewed weekly.

Daily log, Pen num	, weekly r iber:	Daily log, weekly recording sheet Pen number:	heet Colour:										
Day of week	Date	Person /s who record ed	Time if differs from specifi ed	Clean or feed	Kg feed fed	Kg feed wast e	Faecal sample (g) 07:10	Faecal sample (g) 15:45	Temp (C) 12:00 - 13:00	Humid ity 12:00- 13:00	Floor temp (C) 12:00- 13:00	Water temp (C) 12:00-	Comments (piling, illness, death, etc)
Mon				Clean									
Tues				Feed									
wed				Clean									
Thur				Feed									
Fri				Clean									
Sat													
Sun				Feed									



Annex B: Growth measures recording sheet pre-trial (post-trial sheet did not contain TSU column).

	1	1								
	Comments									
	Confirm TSU									
	Confirm skin map									
	Photo number									
	BelW (cm)									
Date:	SVL (cm)									
	TBL (cm)									
	Weight (kg)									
Processing and sorting data collection form Observers name:	Microchip number									
ting data	Pen									
g and sor	Tag colour									
Processing and sc Observers name:	Animal									

Annex C: Skin grading recording sheet

, Grade:	Severity Score								
Size of animal:	Defect								
	Area	ਰ	75	පි	5 6	A1	A3	Flanks	Over the back
, Microchip number:									
Crocodile #:									
Date:	E1	E2 F1	Third Scute Behind the	22 04	Pattern Arr Head Area = Belty Area = Quadrants = Q1-4	A1 A2	Outsi Pattern E1 -E F1- F	Area 4	



Annex D: Behaviour recording sheets based on time-lapse data.

	_ +-						
	Com ment s						
	Piling land						
	Piling wate r						
	Cont act land						
	Cont act wate r						
	Sep land						
	Sep water						
	Wate r clarit y						
	Crocs on land						
	Crocs in wate r						
	Crocs in view						
	Hum an pres ence						
	Feed or clean						
form	Temp (C)						
llection	Photo ID						
Time-lapse (behaviour) data collection form	Density						
oehaviot.	Anim als in pen						
apse (k	Pen						
Time-l	Date						



Annex E: Stress data recording sheet

_	,		1		1	-		
	Comments							
	fGCMco nc (ug/g DW)							
	EIA means (pg)							
	Dilution factor							
	Extraction volume							
	Faecal powder weight (g)							
	Feed or clean day							
	Week of trial							
	Month							
	Date collected							
4	Density							
ng shee	Pen							
Stress data recording sheet	Sample ID							
Stress da	Lab nr							



Annex F (PHOTO PLATE)



Plate 1: An external view of the trial house as viewed from the entrance.



Plate 4: Image of a high-density pen, fully stocked, at the beginning of the trial.



Plate 2: View from the entrance to the crocodile house before the house was stocked for the trial, showing camera placements.



Plate 5: Image of a low-density pen, fully stocked, at the beginning of the trial.



Plate 3: Image of an empty pen, before crocodiles were placed, to show the smooth cement surface and centred water body.

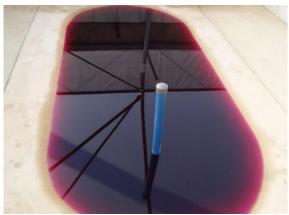


Plate 6: Potassium permanganate treated water in the first week of the trial.



Plate 7: Crocodile during processing, with its maw tied shut with a thick elastic band.



Plate 10: Tissue sampling gun provided by Allflex.



Plate 8: Standing scale and holding crate used for weighing the crocodiles during processing.



Plate 11: Image depicting the hole in the first single scute created by the tissue-sampling gun.



Plate 9: Crocodile placed into the holding crate on the scale.



Plate 12: Coloured cable tie in the tail, for sorting into pens at the beginning of the trial.



Plate 13: The eight cable-tie colours used for tail-tagging, for easier sorting into the pens.



Plate 16: Severely protruding tooth of a crocodile during the pre-trial processing.



Plate 14: Injection of microchip at the base of the crocodiles' tail, on the right-hand side of the body, performed by Prof J.G. Myburgh.



Plate 17: Clipping of a protruding tooth during the pre-trial processing, to avoid unnecessary skin damage during the trial.



Plate 15: Screen of the microchip scanner, showing: time, barcode, session number, total number of scans, and charge of the scanner.



Plate 18: Example of one crocodile skin image, as captured during the skin-grading analyses for every animal.



Plate 19: A crocodile skin thrown over a light table to show the method for grading as it usually occurs post-slaughter.



Plate 20: Picture of skin defect classified as "infection" during the grading process of the current study.



Plate 21: Picture of skin defect classified as "abscess" during the grading process of the current study.



Plate 22: Picture of skin defect classified as "hole" during the grading process of the current study. This defect was deep and hollow, cause unknown.



Plate 23: Picture of skin defect classified as "double scaling" during the grading process of the current study.



Plate 24: Picture of skin defect classified as "scratches" during the grading process of the current study. Both old (healing) and recent scratches can be seen.



Plate 25: Picture of skin defect classified as "wrinkles" during the grading process of the current study. Defect was not known, but made the skin look old/worn.



Plate 26: Picture of skin defect classified as "yellowed scar" during the grading process of the current study.



Plate 27: Picture of skin defect classified as "brownspot" during the grading process of the current study.



Plate 28: Picture of skin defect classified as "teeth marks" during the grading process of the current study, likely caused by a recent bite.



Plate 29: Kimo kistock miniature thermo-hygro datalogger.



Plate 30: Handheld IR thermometer in use during the trial captured by over-head cameras.

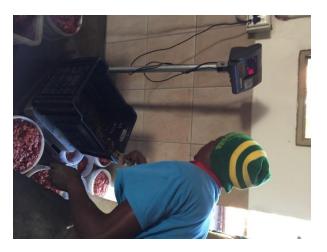


Plate 31: Mixing of the grower diet at the commercial crocodile farm.



Plate 34: An instance of piling of 12 crocodiles during the trial.



Plate 32: Time-lapse image captured during feeding.



Plate 35: Crocodile removed from trial due to severely twisted and infected tail end, presumably due to an aggressive interaction.



Plate 33: Time-lapse image captured during cleaning.



Plate 36: Crocodile with a severe eye infection, randomly sampled from the trial house in September 2017.



Plate 37: Swabbing of an infected crocodile eye (September 2017) after a few crocodiles had been presenting with gooey-eyes.



Plate 38: Swab sample of the floor of a pen near the water's edge (September 2017) after a few crocodiles had been presenting with gooey-eyes, performed by Prof G.E. Swan.



Plate 39: Image of a severe missing tail end from a crocodile that presumably had been in a serious altercation (September 2017) with one or more of its pen mates, crocodile was removed from the trial immediately.



Plate 40: Crocodile being stunned before removal from the pen for post-trial processing, November 2017.



Plate 41: White paint used to mark a crocodile after it had been processed at the end of the trial and placed back into its pen.



Plate 42: Faecal sample (next to a teaspoon) as an example of the size of samples collected, as the trial progressed these faecal samples did increase in size slightly.



Plate 43: Faecal samples stored in a large freezer at Onderstepoort.



Plate 44: Image depicting the faecal samples after pulverisation.



Plate 45: Storage tubes of pulverised faecal samples, stored until analyses could be performed. Notably these tubes held more powder than needed for extraction, remaining samples will be kept in long-term storage at the ERL, Onderstepoort.

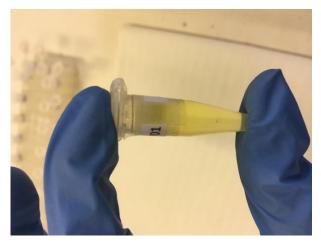


Plate 46: Eppendorf tube containing extracted sample.

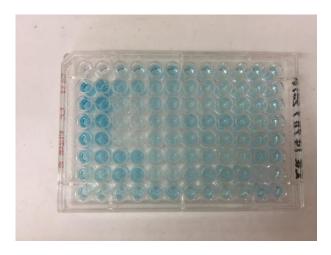


Plate 47: Active FGM plate.



Plate 48: FGM plate after the reaction had been stopped.



Annex G



Animal Ethics Committee

PROJECT TITLE	Farming the Nile crocodile: Optimal stocking density
PROJECT NUMBER	EC070-17
RESEARCHER/PRINCIPAL INVESTIGATOR	D Veldsman

STUDENT NUMBER (where applicable)	U_10120263
DISSERTATION/THESIS SUBMITTED FOR	MSc

ANIMAL SPESIES	Crocodylus Milaticus	
NUMBER OF ANIMALS	261	
Approval period to use animals for research/testing purposes		October 2017 - October 2018
SUPERVISOR	Prof. EC Webb	

KINDLY NOTE:

Should there be a change in the species or number of animal/s required, or the experimental procedure/s please submit an amendment form to the UP Animal Ethics Committee for approval before commending with the experiment

APPROVED	Date 30 October 2017
CHAIRMAN: UP Animal Ethics Committee	Signature (5/2)

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