

https://dspace.org/

Individual behavioural differences in the captive Southern ground hornbill Bucorvus leadbeateri

Young, Lucy Charlotte

2019
https://hdl.handle.net/10539/28911

Downloaded from a DSpace repository. https://dspace.org/

Individual behavioural differences in the captive Southern Ground Hornbill *Bucorvus leadbeateri*



Lucy Charlotte Young

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2019

DECLARATION

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.



Lucy Charlotte Young

29 May 2019

ABSTRACT

Southern ground hornbills (ground hornbill) *Bucorvus leadbeateri* are among Africa's most recognisable birds. The ground hornbill is formally listed as 'Vulnerable to Extinction' on the IUCN Red List and is endangered in both South Africa and Namibia. The ground hornbill is a nationally protected species in South Africa, yet the population numbers are still declining. The species is thus a conservation priority, and studies of captive individuals are needed to assess the suitability of individuals for breeding and potential future release. I investigated the behaviour of five captive populations of ground hornbills in Gauteng Province, and one population in the Western Cape Province, South Africa with the aim of investigating individual behavioural variation in these captive ground hornbills. Firstly, I described nine broad behavioural categories in the captive ground hornbills, and used these behaviours as a basis for further analysis. Secondly, I studied the activity patterns of the captive ground hornbills and found that the ground hornbills in my study did not conform to the bimodal pattern of their free-living counterparts, but rather their activity, at least for the three common behaviours (perching, locomotion, object interaction) remained fairly constant throughout the sampling time. The captive ground hornbills spent the largest proportion of their time perching, followed by locomotion and probing with their beaks. The three behaviours that were displayed the least were thermoregulation, vocalising and feeding. Behaviours varied by location on the overall behaviour but no sex effect. Thirdly, I recorded transactional (behavioural) interaction and found that aggression was rare and occurred in just one population. In contrast amicability was common and occurred more often than chance in three populations. Fourthly, I also found differences in the space use of individuals within populations, where space use was greater in some individuals in each institution. Individuals in each population commonly used less than 50% of their cage, frequently at the same time, linked to feeding, cage composition and their natural patrolling tendencies. Fifthly, I investigated the risk-taking behaviour and found that individuals in each institution varied their behavioural responses inconsistently in a startle test but with some showing consistent responses in novel object tests, indicating personality in ground hornbills. There were also population differences in the responses to a novel object. Finally, correlations among the behaviours indicated that ground hornbills display a behavioural syndrome (i.e. consistent behaviour responses across contexts). These findings allow for a greater understanding of the individual differences in captive ground hornbills, which are important when considering

how individuals are managed and respond to interactions with conspecifics in captivity and for the inclusion in future release programmes.

KEYWORDS: Activity patterns; Animal behaviour; Behavioural syndrome; Risk-taking behaviour; Space use; Southern Ground Hornbill; Transactional behavioural interaction.

ACKNOWLEDGMENTS

Neville Pillay

In previous situations where I have said a ‘Thank You’ speech or written a ‘Thank You’ letter to a group of sponsors, I have been in situations where I don’t know where to start, however when writing this acknowledgement section, it is absolutely clear that the first person to thank is my role model and supervisor, Professor Neville Pillay.

Thank you for your unwavering guidance, support and patience throughout this journey. You are an extraordinary academic, scientist and leader, and I am so honoured to have been able to learn from such a knowledgeable person. Your enthusiasm and passion for biology and behaviour is inspiring and the enjoyment and cohesiveness you encourage in your students is evident in the lab. Thank you for everything Neville, I hope our paths cross again.

Animal Behaviour Lab

Special thanks goes out to Sneha Joshi for all the time and effort she put into reading and editing my drafts. Thank you for your kindness and patience and above all, your knowledge and input into my thesis.

Thank you to Nadine Cronk and Megan Mackay for all your support and proof reading and commenting on my drafts.

Thank you to Candice Neves, Daisy Tlou Raphela, Shanan Atkins, Charne van Niekerk, Leon Kotze and Kirsty Hartman, for your friendship and for putting up with my long and intricate life stories. You are all so unbelievably talented and smart and I am so honoured to have been able to learn from you. I am going to miss you all so much.

Mabula Ground Hornbill Project

Thank you to everyone who was at the 2nd Southern Ground-Hornbill PHVA seminar. I really enjoyed being part of such a passionate and knowledgeable group of scientists and conservationists. Your passion for the Southern Ground Hornbill is inspiring and I really learnt so much.

I would like to say a special thank you to Dr. Lucy Kemp, for introducing me to Southern Ground Hornbill, for all her support and guidance in the topic as well as with helping me

network with all the people within the Southern Ground Hornbill community. Lucy, your assistance was invaluable to me.

Captive Institutions

I would like to say a massive thank you to Grace Nkgweng (Johannesburg Zoo), Kara Heynes (Lory Park), Hendrik Louw (WOB), and Elaine Reeve (Montecasino Bird Gardens) for allowing me to sit for hours observing and collecting data from your Ground Hornbills. This project would not have been possible without your support.

Family and Friends

Last but certainly not least, I would like to thank my incredible family, Sally Young, Mark Young and William Young, as well as my amazing friends Alexandra Gilbert, Ridha Moosa, Stephanie Schoeman and Yvonne Perkins for being there for me throughout this journey.

National Research Foundation

Thank you to the National Research Foundation (NRF) for your financial support. The experimental protocol was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand, clearance certificate number AESC 2017/05/32/B.

TABLE OF CONTENTS

Declaration……ii

Abstract……iii

Acknowledgments……v

Table of contents……...vii

List of figures……...ix

List of tables……xii

List of pictures……xiv

Introduction……15

Animal Personality……15

Behavioural Syndromes……16

Measuring Personality……17

Personality of Captive Animals……20

Human management……20

Size and complexity of space……21

Frequent presence of zoo visitors……23

Southern Ground Hornbill……24

Social organization……25

Territories……25

Diet……26

Diurnal activity patterns……27

Why study the Southern Ground Hornbill? ……27

Gap in our knowledge……28

Aims, objectives and predictions……29

Materials and methods……31

Study subjects and housing……31

Protocol and Design……43

The broad behavioural categories of captive ground hornbills……43

The diurnal activity patterns of captive ground hornbills……43

The transactional (two-way social) interactions of captive ground hornbills……..….44

The space use and exploratory behaviour of captive ground hornbills…….……...45

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle…….…..46

The behavioural syndrome in captive ground hornbills……48

Data analyses……...……..49

Results……...……51

The broad behavioural categories of captive ground hornbills……..……51

The diurnal activity patterns of captive ground hornbills……..……59

The transactional (two-way social) interactions of captive ground hornbills..……..…63

The space use and exploratory behaviour of captive ground hornbills……..……68

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle……..81

The behavioural syndrome in captive ground hornbills…….……94

Discussion…….……97

The broad behavioural categories of captive ground hornbills…….97

The diurnal activity patterns of captive ground hornbills…….97

The transactional (two-way social) interactions of captive ground hornbills...…….99

The space use and exploratory behaviour of captive ground hornbills……..100

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle……..101

The behavioural syndrome in captive ground hornbills……102

Conclusion……103

Supplementary Graphs…..……..104

References……...114

LIST OF FIGURES

Figure 1: Distribution map of the Southern Ground Hornbills *Bucorvus leadbeateri*……..25

Figure 2: A map of South Africa showing the two provinces and four locations where studies were conducted…….31

Figure 3: An aerial depiction of the Johannesburg Zoo Public display enclosure of Southern Ground Hornbill. …… 34

Figure 4: An aerial drawing of the Johannesburg Zoo Hidden display enclosure of Southern Ground Hornbill showing the layout of the plants, nest boxes and perching areas…… 36

Figure 5: An aerial drawing of the Lory Park Southern Ground Hornbill enclosure showing the layout of the plants, nest boxes and perching areas……. 38

Figure 6: An aerial drawing of the Monte Casino Bird Park Left and Right enclosures housing Southern Ground Hornbill, showing the layout of the nest boxes and perching areas. ……39

Figure 7: An aerial drawing of the Hout Bay World of Birds Southern Ground Hornbill enclosures showing the layout of the nest boxes and perching areas…… 41

Figure 8: A diagrammatic representation of the 12 zones (for the ground hornbill enclosures at the Johannesburg Zoo, Lory Park and Monte Casino Bird Gardens, and longitudinal divisions…… ……45

Figure 9: The large metal garden chair used in novelty object tests for ground hornbills… 48

Figure 10: Percentage of time devoted to 9 behaviours by 18 captive ground hornbills *Bucorvus leadbeateri* in Gauteng and the Western Cape provinces…….59

Figure 11: The 12 hour activity-time profile of perching, interaction with an object and locomotion in 18 captive ground hornbills……60

Figure 12: The frequency recorded for 9 categorises of behaviours in six captive ground hornbill populations, in the Gauteng and Western Cape provinces of South Africa…….62

Figure 13: A diagrammatic representation of the space use by three ground hornbills in 12 zones of the Johannesburg Zoo hidden display enclosure…….70

Figure 14: A diagrammatic representation of the space use by three ground hornbills in 12 zones of the Johannesburg Zoo public display enclosure…….72

Figure 15: A diagrammatic representation of the space use by two ground hornbills in 12 zones of the Monte Casino Bird Gardens right enclosure display enclosure……..……..75

Figure 16: A diagrammatic representation of the space use by two ground hornbills in 12 zones of the Monte Casino Bird Gardens left enclosure display enclosure…….77

Figure 17: A diagrammatic representation of the space use in 12 zones of the Lory park enclosure display enclosure…….80

Figure 18: The comparison of the latency (total duration) to resume normal activity by ground hornbills in 6 enclosures…….81

Figure 19: The latency (total duration) to resume normal activity between the two sexes in all institutions……..….81

Figure 20: The latency (total duration) to resume normal activity by ground hornbills in three replicates……..82

Figure 21: The latency (total duration) to resume normal activity by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates……..82

Figure 22: The latency (total duration) to resume normal activity by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates……83

Figure 23: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Monte Casino Bird Gardens Right Enclosure in three replicates….84

Figure 24: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Monte Casino Bird Gardens Left Enclosure in three replicate…….84

Figure 25: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Lory Park Enclosure in three replicates…….85

Figure 26: The latency (total duration) to resume normal activity by the six individual ground hornbills at the World of Birds Enclosure in three replicates……..85

Figure 27: The latency (total duration) to approach the novel object by ground hornbills in in the 6 enclosures……86

Figure 28: The latency (total duration) to approach the novel object by the two ground hornbill sexes. ……86

Figure 29: The latency (total duration) to approach the novel object by ground hornbills in the three replicates. ……87

Figure 30: The latency (total duration) to approach the novel object by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates……88

Figure 31: The latency (total duration) to approach the novel object by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates……88

Figure 32: The latency (total duration) to approach the novel object by two three individual ground hornbills at the Monte Casino Bird Gardens Right Enclosure in three replicates….89

Figure 33: The latency (total duration) to approach the novel object by the two individual ground hornbills at the Monte Casino Bird Gardens Left Enclosure in three replicates….. 90

Figure 34: The latency (total duration) to approach the novel object by the two individual ground hornbills at the Lory Park Enclosure in three replicates……90

Figure 35: The time spent by ground hornbills interacting with the novel object in the 6 locations……..91

Figure 36: The time spent by ground hornbills interacting with the novel object in the two sexes……91

Figure 37: The time spent by ground hornbills interacting with the novel object in three replicates observations……92

Figure 38: The time spent with the novel object by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates……92

Figure 39: The time spent with the novel object by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates…….93

Figure 40: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates……94

Figure 41: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates……94

Figure 42: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates…….95

LIST OF TABLES

Table 1: Demographic data for the 18 Southern Ground Hornbills studied in four locations, three in Gauteng Province and one in the Western Cape Province……33

Table 2. The behaviours recorded in the ground hornbill individuals at the four locations in Gauteng and the Western Cape provinces……..52

Table 3: Socio-metric matrix of the amicable interactions between the three individuals in the Joburg Public enclosure……..……64

Table 4: Socio-metric matrix of the amicable interactions between the three individuals in the Joburg Hidden enclosure…….64

Table 5: Socio-metric matrix of the aggressive interactions between the three individuals in the Joburg Hidden enclosure……65

Table 6: Socio-metric matrix of the amicable interactions between the two individuals at Lory Park……...65

Table 7: Socio-metric matrix of the amicable interactions between the two individuals in the Monte Right enclosure…….66

Table 8: Socio-metric matrix of the amicable interactions between the two individuals in the Monte Left enclosure…… 66

Table 9: Socio-metric matrix of the amicable interactions between the six individuals at the Hout Bay World of Birds……..…….67

Table 10: Socio-metric matrix of the aggressive interactions between the six individuals at the Hout Bay World of Birds……..67

Table 11: The frequency of occurrence by three ground hornbills in 12 zones in the Joburg hidden enclosure…… 68

Table 12: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Joburg Hidden enclosure…….……69

Table 13: The frequency of occurrence by three ground hornbills in 12 zones in the Joburg public enclosure……71

Table 14: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Joburg Public enclosure……72

Table 15: The frequency of occurrence by two ground hornbills in 12 zones in the Monte Right enclosure…….……...73

Table 16: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Monte right enclosure……74

Table 17: The frequency of occurrence by two ground hornbills in 12 zones in the Monte Left enclosure……...76

Table 18: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Monte Left enclosure…….77

Table 19: The 12 zones in the Lory Park…….78

Table 20: The frequency of occurrence by two ground hornbills in 12 zones in the Lory Park enclosure……...79

Table 21: The correlations between the variables scored in the general behaviours observations, sociality observations, space use observations and risk taking behaviour tests……...96

LIST OF PICTURES

Picture 1: An example of perching behaviour…….……53

Picture 2: An example of walking behaviour.…….54

Picture 3: An example of flying behaviour…….55

Picture 4: An example of social (allo-preening) behaviour…….56

Picture 5: An example of preening behaviour. ……...57

Picture 6: An example of feeding behaviour. ……...……..57

Picture 7: An example of thermoregulatory behaviour……58

INTRODUCTION

Anyone who spends even a little bit of time in nature and observes the behaviour of animals in their natural habitat will see that it is very apparent that individual animals behave in very different ways, even within a uniform group. For example, if you were to observe pigeons *Columbidae* in a park, you may observe an aggressive encounter between two individuals, or amicable interactions such as allo-preening between another pair. You may also observe a single individual far out in the field by itself, or some individuals approaching and remaining in close proximity to you and other human observers. If you, observed the flock of feral pigeons over a long period of time, you would notice that individuals do not only differ in their behaviour, but that these differences are also repeatable over time and across different contexts. In humans, these behavioural differences among individuals are referred to as personality types (Pervin and John 1999), whereas in non-human animals these differences are also referred to as behavioural tendencies or behavioural axes (Gosling 2001; Dall *et al.*, 2004; Sih *et al.* 2004).

Animal Personality

Understanding how and why individual variation in behaviour is maintained in a population, from an evolutionary and ecological perspective, is an important field of research (Réale *et al.* 2007; Kluen *et al.* 2012; Carere and Maestripieri 2013; Torgerson-White and Bennett 2014; Yuen *et al.* 2016). Animal personality (hereafter personality) is described as the variation in individual behaviour that is repeatable over time and across contexts (Réale *et al.* 2007; Kluen *et al.* 2012; Carere and Maestripieri 2013; Torgerson-White and Bennett 2014). For example, individuals within a species will often differ in their aggressive behaviour (Riechert and Hedrick 1993; Huntingford 1994), although they may alter their aggression levels slightly in different contexts, while maintaining their levels of aggression relative to other conspecifics (Dall *et al.*, 2004). Correlations have been found for activity (Sih *et al.* 2003), exploration (Dingemanse *et al.* 2002) and as risk-taking (Fraser *et al.* 2001) behaviours. This consistency of behavioural variation is present in a wide range of invertebrates, such as hermit crabs *Pagurus bernhardus* (Briffa *et al.* 2008), the common periwinkle *Littorina littorea* (Seaman and Briffa 2015), dumpling squids *Euprymna tasmanica* (Sinn and Moltschaniwskyj 2005), and vertebrates such as the pumpkinseed sunfish *Lepomis gibbosus* (Wilson *et al.* 1993), sticklebacks *Gasterosteus aculeatus* (Bell and Stamps 2004), and spotted hyena *Crocuta crocuta* (Gosling 1998). Moreover, such variation

has been observed in natural and captive populations (Gosling, 2001; Sih *et al.*, 2004; Réale *et al.*, 2007).

Personality may be fixed and can indicate reduced behavioural plasticity (Sih *et al.*, 2004). However, some studies show that personality does not preclude plasticity (Yuen *et al.* 2015), and individuals may have a flexible response in different contexts, but that their rank remains the same compared to their conspecifics in the different contexts. In nature, personality types in a population occur either because of the selection for multiple traits (assuming that they are heritable) or because they are emergent properties of the individuals in a group. For example, in Icelandic horses (*Equus caballus*) being aggressive in a group depends on which other individual displays less aggressive tendencies (Vervaecke *et al.*, 2007). The adaptive explanations of personality and broadly consistent behavioural differences are addressed by a large number of well-developed studies (e.g. Dall *et al.*, 2004; Dingemanse and Réale, 2005; Réale *et al.*, 2007; Wolf *et al.*, 2008; Stamps and Groothuis, 2010; Wolf and Weissing, 2012; Sih *et al.*, 2015). The majority of studies explain that personality is an adaptive outcome of the combination of the underlying differences in an animal's state (internal and external) and its state-dependent behaviours (Sih and Bell 2008; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010; Sih *et al.*, 2015). State is a broad term that describes the traits of an animal that affect the costs and benefits of its behavioural actions (Houston and McNamara, 1999; Dall *et al.*, 2004). State therefore does not just refer to genes, sex, age and energy, but also experience, the ecological context, and behaviour during previous social interactions (Sih *et al.*, 2004a, b; Sih and Bell, 2008; Wolf *et al.*, 2008).

Behavioural Syndromes

Behavioural syndromes describe correlations between functionally different behaviours across different contexts in individuals, such as between risk taking in a novel environment and high aggression levels to conspecifics (Sih *et al.* 2003; Dingemanse *et al.*, 2007). Behavioural syndromes are the correlation between functionally different behaviours and have been investigated in an array of different tests such as the activity and inactivity of individuals, social motivation, and measures of risk taking (Wilson 1998; Fraser *et al.* 2001; Dingemanse *et al.* 2002; Drent *et al.* 2003; Sih *et al.* 2003). There is increasing evidence of individuals that show correlated behavioural traits that can be measured across multiple contexts (Wilson 1998; Fraser *et al.* 2001; Dingemanse *et al.* 2002; Drent *et al.* 2003; Sih *et al.* 2003). For example, Huntingford (1976) showed that individual sticklebacks

Gasterosteidae spp. that were active in a novel environment were also bolder in the responses towards predators as well as aggressive towards conspecifics. In another example, Wray *et al.* (2011) studied the collective personality and consistent differences in colonies of honeybees *Apis mellifera*, and found consistent behavioural differences in defensive responses and foraging which were strongly tied to colony productivity and winter survival. Also, individuals in colonies of bees showed consistent behavioural differences in traits such as defensive responses and foraging activity (Wray *et al.* 2011).

Behavioural syndromes have important ecological influences which result in trade-offs between different behaviours (Sih *et al.* 2004a, b; Dingemanse *et al.*, 2007). Correlations between boldness and aggression, for example, could benefit an individual during competition for resources, such as mates or territory, but could be detrimental in situations where high levels of aggression are disadvantageous, such as during high predation risk or offspring care (Sih *et al.* 2004b; Bell and Stamps 2004). Individuals may differ in the way they perceive and respond to stressors (i.e. broadly defined as a challenge to an animal) which could ultimately reflect the differences in their personalities (Dall *et al.* 2004). Thus, personality studies have provided a useful insight into how individual animals cope with environmental challenges and stressful circumstances (Dall *et al.* 2004; Yuen *et al.* 2016).

Although personality is the measurement of individual variation within-populations, it may still vary between populations, since individuals experience different pressures in different environments (Réale *et al.* 2000). For example, Eurasian minnows *Phoxinus phoxinus* that lived in a tributary where the predation risk and parasitism were high showed a higher average boldness and lower activity levels than the fish living in a low predation and parasitism risk population (Kortet *et al.* 2015; Kortet *et al.* 2010). Similarly, other studies on fish, such as the creek chub *Semotilus atromaculatus,* Atlantic silverside *Menidia menidia,* and tropical poeciliid *Brachyrhaphis episcopi,* showed that populations that experienced higher levels of predation tended to be bolder than fish from populations with lower levels of predation (Fraser *et al.* 2001; Brown and Braithwaite 2005).

Measuring Personality

The five most commonly considered personality axes include boldness-shyness (responses to a risky situation), exploration-avoidance (reaction to novelty), the activity level of an animal, aggressiveness as well as sociability (i.e. response to conspecifics; Réale *et al.* 2007; Yuen *et*

al. 2016). Of these personality measures, shyness-boldness is most commonly studied (Carere *et al.* 2005; Yuen *et al.* 2016). This is because boldness can be associated with antipredator behaviour (Brown and Braithwaite 2005), mate choice (Godin and Dugatkin 1996), population dispersal (Fraser *et al.* 2001), and survival (Réale *et al.* 2000) and therefore covers a wide range of research topics. Boldness is defined as the willingness of an individual to engage in risk-taking behaviour (Réale *et al.* 2007; Sinn *et al.* 2010; Yuen *et al.* 2016). A bold individual will typically exhibit a short latency to resume normal activities when disturbed by a threatening event (Réale *et al.* 2000; Brown *et al.* 2005; Briffa *et al.* 2008; Yuen *et al.* 2016). In contrast, a shy (less bold) individual will show risk-averse behaviour and exhibit a long latency to resume normal activities when disturbed by a threatening event (Réale *et al.* 2000; Brown *et al.* 2005; Briffa *et al.* 2008; Yuen *et al.* 2016). Boldness has been measured using a variety of methods, such as measuring the time spent in the centre of open field tests (e.g. guppies *Poecilia reticulata*; Burns 2008) and startle tests (e.g. two-spotted gobies *Gobiusculus flavescens*; Magnhagen *et al.* 2014).

Exploratory behaviour is another widely studied personality axis (Réale *et al.* 2007; Sih and Bell 2008; Carere and Maestripieri 2013). Exploration is usually associated with locating resources, as well as territorial patrolling within a particular environment, which ultimately maximises fitness under the specific conditions of that particular environment (Hughes 1997; Carere and Maestripieri 2013). Habitats differ in terms of food abundance, distribution and availability (Wolf *et al.* 2008) as well as predation risk (Bell and Sih 2007), so that exploration of an environment might be context dependent (Carere and Maestripieri 2013). Dingemanse *et al.* (2002) investigated the exploratory behaviour of individual great tits, *Parus major*, in novel environments and showed that there was a significant consistency in the individual variation in open field behaviour, and that the behavioural variation was heritable. Exploration can be measured by the amount of locomotion an animal does in an open field and the willingness to venture into an exposed area.

The ability to gather information and assess risks in novel environments is crucial for survival (Augustsson and Meyerson 2004). Risk taking can be measured in several ways, with a neophobic response to a novel object (Mowles *et al.* 2012) and the recovery after a startle (Yuen *et al.* 2016) being common metrics. In such tests, bolder individuals are those that display reduced neophobia and more rapid resumption of "normal" activity following a startle (Yuen *et al.* 2016). Exploration is usually measured in novel environments (Niemela *et al.*

2012). The level of exploration of a novel environment is also a reflection of the risk-taking behaviour of an individual and is strongly correlated to predation presence (Carere and Maestripieri 2013). Augustsson and Meyerson (2004) studied the exploration and risk assessment of wild house mice *Mus musculus* and two domesticated house mice strains, and found differences in behavioural strategies related to risk assessment and risk taking among wild mice versus domesticated house mice. Wild mice were more cautious than domesticated mice before entering a novel zone but explored all zones after the risk assessment (Augustsson and Meyerson 2004). Van Oers *et al.* (2004) showed that individual great tits *Parus major* that were selected from a 'fast' exploration line returned quickly to the feeding table with mealworms compared to the individuals selected from a 'slow' exploration line after being startled.

Because some individuals are likely to be consistently more active than others across various situations (Houston and McNamara 1999; Sih *et al.* 2003), these individuals need to trade-off between competing activities. For example, greater activity is possible in the absence of predators. However, greater activity can incur costs in the presence of predators (Houston and McNamara 1999; Sih *et al.* 2003). Often individuals are faced with conflicting selection pressures that arise because of time activity budget conflicts (Sih *et al.* 2003). For example, time spent in an activity, such as feeding, can result in reduced time spent in other activities such as predator avoidance or mate searching (Houston and McNamara 1999; Sih *et al.* 2003). Some individuals are likely to decrease their activity in the presence of predators, or increase their activity when they experience hunger. Periquet *et al.* (2010) studied vigilance by individual greater kudu *Tragelaphus strepsiceros* while drinking at a waterhole and in the presence of lion, and found that individual kudu adjusted their vigilance level significantly in the presence of predators, devoting significantly higher proportion of time to vigilance when lions were in the vicinity. The results also showed that the proportion of time spent on individual vigilance decreased as group size increased as well as the presence of other herbivores at the waterhole (Periquet *et al.* 2010).

Sociability and aggressiveness are personality axes considered within the context of the social relationships and behaviours between group members (Carere and Maestripieri 2013). The behaviour of a group of individuals can be affected by the mix of personality types present within the group (Kurvers *et al.* 2009; Carere and Maestripieri 2013). Aggression towards conspecifics is often used to settle disputes over limiting resources and is also important in

dominance disputes (Carere and Maestripieri 2013) and territorial behaviour (Duckworth 2006; Carere and Maestripieri 2013). Verbeek *et al.* (1996) showed that, in great tits, aggressive behaviour was consistent over time for an individual and was strongly correlated with an individual's boldness and exploration: individuals that were faster explorers started more fights than the slow explorers, and tended to win the fights they initiated. Adult male rhesus macaques *Macaca mulatta* show high levels of predictability between sociability (which was positively associated with number of approaches initiated and received) and a greater tendency to engage in affiliative and amicable interactions (Capitanio 1999). The results also showed that sociability was strongly related to size of the kin network in the animals' natal groups (Capitanio 1999).Personality is also predicted by life history variables, such as sex and age (Øverli, *et al.*, 2006). For example, female rats *Rattus rattus* displayed a greater curiosity for novel objects and environments, showed higher levels of exploration as well as lower levels of anxiety, than males (Aguilar *et al.*, 2003). Macrì *et al.* (2002) showed that risk taking behaviour during exploration of a plus-maze is greater in adolescent than in juvenile or adult mice *Mus musculus*. The behaviour in novel and stressful situations differed between immature male and female rainbow trout (*Oncorhynchus mykiss*) for example, when placed into a novel facility, females resumed feeding quicker after transfer than males (Øverli, et al., 2006).

Personality of Captive Animals

In captivity, the combination of personality types in conspecifics can be chosen by artificial selection. The behaviour of captive animals is shaped by several, often interconnected, factors (Hemsworth, 2003). Hosey (2005) proposed three variables that distinguishes a zoo environment from natural environments: 1) human management; 2) size restriction and complexity of space; and 3) frequent presence of zoo visitors. These factors could influence the personality types of captive animals.

Human management

The first obvious difference between zoo animals and their free-living counterparts is the fact that they are managed in some way by humans. It would be an obvious assumption that non-aggressive animals are favoured and selected for in captive environments for easier management (i.e. avoiding caretaker or visitor injury; Anderson *et al.* 2003). Keeper-animal interactions usually involve cage cleaning, daily feeding, general routine health examinations

as well as transportation of animals. Avoiding animal aggression towards humans (keepers and visitors) in captive environments is one of the main priorities of captive institutions (Hemsworth, 2003; Hosey 2005). Aggression in animals can arise from many different factors. A basic fear of humans is one of the drivers of aggression (fear-induced aggression) in many animals (Hemsworth, 2003). In a study done at the Atlanta Zoo petting zoo (Atlanta, USA), Anderson *et al.* (2002) found that Romanov sheep *Ovis aries*, which were usually slightly fearful of humans, displayed higher aggression and avoidance behaviours to the human visitors, compared to the naturally amiable pygmy goats *Capra aegagrus hircus* which were selected for and favoured in the petting zoo. Likewise, Thompson (1989) studied the responses of 12 different ungulate species towards zoo keepers in a captive environment, and showed that there were higher levels of vigilance towards the keepers when the keepers were present inside than outside the enclosure. The results suggest that the increased vigilance levels resemble an anti-predator response and that the animals viewed keepers as potential predators (Thompson, 1989; Hemsworth, 2003; Hosey 2005).

Selective breeding of amicable individuals and the relocating of aggressive individuals' offsite are common human management techniques. However, positive reinforcement techniques can reduce aggressiveness in individuals of some species and thereby reduce the risk of injury and result in an overall more amicable interaction. Mitchell *et al.* (1991) found that golden-bellied mangabeys *Cercocebus chrysogaster* at the Sacramento Zoo, USA displayed higher levels of aggression towards visitors and far less threats and aggression directed at keepers and researchers, highlighting differences in their responses to familiar and unfamiliar people. Melfi and Thomas (2005) found that colobus monkeys *Colobus guereza* at Paignton Zoo, UK, expressed different behaviours and interactions (amicable, aggressive or neutral) with keepers, zoo staff and zoo visitors; in particular, increased handling time and positive reinforcement, used to train the monkeys for general routine examinations, significantly reduced aggressive interactions with humans (Melfi and Thomas, 2005).

Size and complexity of space

Most animals have restricted space in captivity compared to their natural environment (Rhoads and Goldsworthy, 1979; Finlay *et al.*, 1988). Previous studies have shown that crowding (a reduced physical space or an increase in the density of animals) is strongly correlated with increased levels of aggression. For example, Southwick and Siddiqi (1998)

reduced the living space of captive rhesus monkeys, resulting in increased aggression in the troop. Similarly, Alexander and Roth (1971) found increased levels of aggression in Japanese macaques *Macaca fuscata* under restricted space. Nevertheless, aggression in chimpanzees *Pan troglodytes* rose only slightly when they were crowded, and they used various social behaviours to maintain amicable relationships when exposed to crowding-induced stress (Nieuwenhuijsen and de Waal 1982). Extensive research has been done subsequently on the behaviours that different animals, particularly primates, use to avoid aggression in restricted space (deWaal, 1989; deWaal *et al.*, 2000). In one study, Duncan *et al.* (2013) showed that two chimpanzee *Pan troglodytes* groups used a tension-reduction tactic (behaviours used by an individual to reduce, deny, or escape from a threat or any physical or emotional distress) to limit aggression in an unrestricted outdoor environment. When the two groups were housed in restricted high-density conditions for a prolonged period of a few months, there were significant increases in abnormal behaviour and this resulted in the group of chimpanzees adopting a tension-reduction tactic, while the other group adopted a conflict-avoidance tactic to limit aggression under high spatial density (Duncan *et al.*, 2013).

The available space is not the only variable that affects the behaviour of animals. Several studies have shown that the complexity and the contents within a space is as important in shaping behaviours as cage size (Wilson 1982; Perkins 1992; Mallapur *et al.* 2005). For example, Mallapur and Chellam (2002) found that stereotypical pacing and the activity budget of Indian leopard *Panthera pardus* in four zoos in southern India were not influenced by the presence of visitors nor by the feeding time but rather by enclosure features and size: higher levels of stereotypic pacing were exhibited in the small, low enrichment off-exhibit enclosure than in the large high- enrichment on-exhibit enclosure. Similarly, in Orangutans (Bornean orangutan *Pongo pygmaeus* and the Sumatran orangutan *Pongo abelii*), Perkins (1992) showed that enclosures containing many movable objects as well as ample social opportunities, promoted the highest levels of activity in the orangutans.

The behaviour of captive animals can be influenced by cage structure and interactions with conspecifics. Directly or indirectly, studies have suggested that the regular movement of captive individuals from one enclosure to another increases the overall activity and encourages behaviours that occur in non-captive populations of the same species (Lukas *et al.*, 2003; White *et al.* 2003). In a study of 13 captive western lowland gorilla *Gorilla gorilla*, Lukas *et al.* (2003) found that, in response to systematic rotation between zoo enclosures, the

gorilla showed an increase in enclosure use and reduced negative self-directed behaviour. Furthermore, the gorillas increased their locomotion, social distance, use of grass areas and overall daily activity, suggesting that frequent change in the captive environment promotes a wider behavioural repertoire (Lukas *et al.* 2003). The proximity to other species, for example, exposure to the scents of natural predators, can also have a significant effect on the stress levels and behaviour of captive animals. For example, cotton-top tamarin *Saguinus oedipus* showed a noticeably greater anxiety response to faecal scents of their predators (Margay *Leopardus wiedii* and Tayra *Eira barbara*) compared to scents of their non-predators (capybara *Hydrochoerus hydrochaeris* and paca *Cuniculus paca*) (Buchanan-Smith *et al.*, 1993).

In many captive situations, individuals experience regular changes to their group composition and membership, imposed by humans, leading to behavioural changes associated with a change in the social environment (Reinhardt 1990; Reinhardt *et al.*, 1995). Examples of changes to captive groups include the merging of two or more already established groups in the common chimpanzee *Pan troglodytes* (Seres *et al.*, 2001), introducing new individuals into existing groups in lowland gorillas *Gorilla* (Hoff *et al.*, 1996; Brent *et al.*, 1997) and introducing individuals to each other prior to introducing both into an existing group in ring-tailed lemur *catta* (Meshik, 1999). Reinhardt and colleagues (1988) studied the behavioural responses of singly housed female rhesus monkeys and found that 50% of the pairs exhibited aggression towards each other, while 50% engaged in amicable social grooming or hugging. Yet, 83% of the pairs were compatible later, with none of the partners showing signs of depression and none showing serious injury; the remaining 7% of the pairs were incompatible (two cases of depression, one serious tail injury) and were separated (Reinhardt *et al.* 1988).

Frequent presence of zoo visitors

It is easy to assume that the presence of human visitors has an effect on the behaviours of captive animals in the zoo. The noise and visual disturbance levels change dramatically when visitor numbers fluctuate (Hosey 2005). Hediger (1970) showed that zoo animals perceive human visitors in a variety of ways: some animals view visitors as a predator; some as prey; others regard visitors as part of the inanimate environment; and some consider humans as members of their own species. Specifically, long-billed corella *Cacatua tenuirostris* were motivated to interact with human visitors, with some behaviours only performed in the

presence of people (Nimon and Dalziel 1992). In contrast, cheetah *Acinonyx jubatus* did not alter their behaviours in the presence or absence of visitors (O'Donovan *et al.* 1993).

Southern Ground Hornbill

The Southern Ground Hornbill *Bucorvus leadbeateri* (hereafter referred to as ground hornbill) is one of nine species of African savanna hornbills and one of two species in the family Bucorvidae - the other being the Northern Ground Hornbill *Bucorvus abyissincus* (Vigors 1825; Kemp and Kemp 1980; Zoghby 2015). Ground hornbills are large birds with black plumage, black legs and bill and bare facial skin around the eyes and throat (Kemp and Kemp 1980). Adult body length is 90-130 cm and they weigh roughly 4 kg (Kemp and Kemp 1980; Kemp 1995; Theron 2011; Zoghby 2015). The sex and the age of the ground hornbills can be distinguished by the colour of the bare throat, with adult males having a bright red colour, adult females having a patch of deep violet-blue under the base of the lower mandible, and juveniles, younger than 6 years old, having either a black/dark blue or yellow throat colouration (Kemp and Kemp 1980).

The distribution also covers large parts of South Africa, Zimbabwe, Botswana, Mozambique and Malawi with some occurrence in Namibia. The ground hornbill distribution within eastern and northern South Africa is widespread but sparse, extending from Limpopo Province, through Mpumalanga and KwaZulu-Natal to the Eastern Cape provinces (Kemp 2005) (Figure 1). However, the largest concentrations fall into the boundaries of extensive conservation areas such as the Kruger National Park and private reserves in northern and eastern South Africa (Tarboton et al. 1980). Populations are significantly less vulnerable to decline in areas where anthropogenic threats are absent or minimal (Chiweshe, 2007; Broms et al., 2014; Kemp 2017).

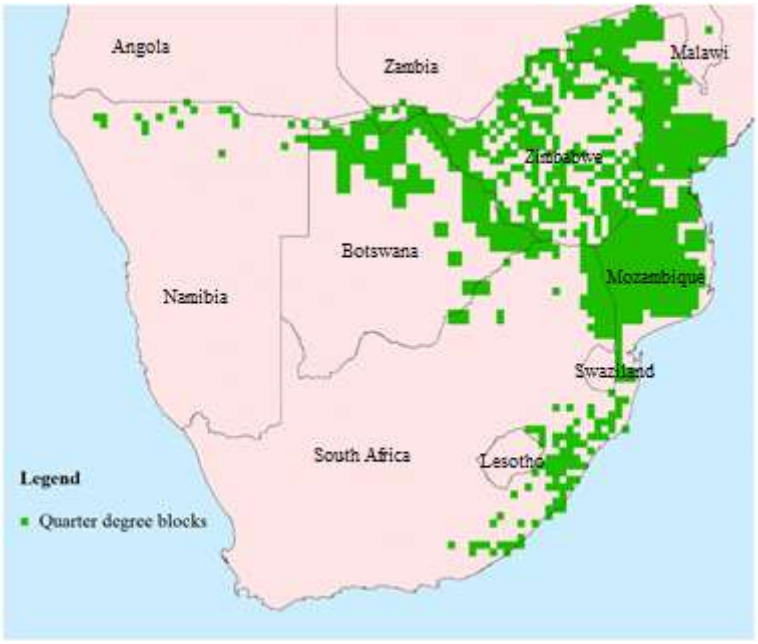


Figure 1: Distribution map of the Southern Ground Hornbills *Bucorvus leadbeateri*. The map shows the coverage on a pentad scale. A 5 minute x 5 minute coordinate grid super-imposed over the continent for spatial reference. (Source: http://sabap2.adu.org.za)

Social organisation

Kemp and Kemp (1980) generated foundational knowledge on behaviour and ecology of free-living ground hornbills, with little or no other reported literature on ground hornbills. I have used their results extensively below. The social organisation of the ground hornbill is complex. It is monogamous but lives in social groups of 2-8 members which comprise of an alpha breeding pair assisted by 2-5 adult males and 2-4 immature individuals of both sexes ('helpers' assist the breeding pair with defending the territory and rearing the chick) (Kemp and Kemp 1980; Kemp 1995; Zoghby 2015). In populations in the Kruger National Park, ground hornbills lived in cohesive units consisting of three to five birds throughout the year. The age and sex composition of groups varied considerably, and within mixed sexed groups, adult males outnumbered adult females. In their observation of 55 birds, seven females, but only one male, were recorded living alone and not in a group. The solitary individuals either lived on the borders or just within the territory borders of other groups but foraged and slept alone (Kemp and Kemp 1980).

Territories

The ground hornbill groups are territorial, with groups occupying large exclusive areas, averaging 100 km^2 per group, which normally occur over well grazed areas and water points (Kemp and Kemp 1980; Kemp 1995). Territorial calling most commonly occurred every morning before sunrise (unless it was raining) and continued for 2-50 min (Kemp and Kemp, 1980). When an individual trespassed into a neighbouring territory, it became alert, had a high vigilance frequency when feeding, and flew back immediately to its territory after encountering an individual of the neighbouring group (Kemp and Kemp 1980). Territorial defence characteristically involved high aerial chases until the intruder had returned to its territory, and once in the safety of its own boundary, both individuals would either perch quietly or would call at the neighbouring members sometimes as close as 100m away (Kemp and Kemp 1980).

The ground hornbill is a K-selected species with a very low reproductive output, coupled with a high survival rate (Kemp, 1976; Kemp and Kemp, 1991; Zoghby 2015). Breeding occurs seasonally and is normally initiated by food availability and the first heavy summer rains (Kemp and Kemp, 1991; Zoghby 2015). Clutch size is normally 2 eggs which are laid 3-5 days apart (Kemp, 1976; Kemp and Kemp, 1991; Zoghby 2015). Typically, only one chick fledges per season. In the case of two eggs hatching, the second chick normally dies from malnourishment due to parental neglect and competition with its older, larger sibling (Kemp and Kemp, 1980).

Both male and female juveniles remain in the group until they are approximately two years old and are dependent on the group for protection and food for at least the first 6 months of their life (Morrison *et al.*, 2005; Theron 2011). At approximately 2-3 years old, the female juvenile disperses from the group, whilst the male offspring remain in the group as helpers. Ground hornbills reach maturity at an estimated age of 5-6 years for both males and females (Morrison *et al.*, 2005; Theron 2011).

Diet

The two species of ground hornbill are the only hornbills in the family *Bucerotidae* that are entirely carnivorous. Free-living ground hornbills mainly feed on reptiles, amphibians, snails and insects, but can eat prey up to the size of hares (Kemp and Kemp, 1980; Kemp 1988). Kemp and Kemp (1980) analysed the diet of ground hornbill in the Kruger National Park

(2730 feeding records) and showed that virtually all the food was obtained terrestrially, with the items being obtained by either chasing, catching, digging for or scratching for them with the stout bill.

Diurnal activity patterns

Kemp and Kemp (1980) reported that at first light, ground hornbills flew down from their tree roosts and spent most of the day on the ground, mainly foraging. Walking decreased towards midday when groups spent time resting and then increased again later in the day. Flying occurred mostly in the first hours of the day, along territorial boundaries and to feeding areas. Flying during the day or in the evening was usually associated with moving into trees to rest or roost at sunset (Kemp and Kemp, 1980). Groups were active for an average of 13 hours during the summer months, spending an average of 70% of their day walking and the rest of the time was spent resting. The stress of overheating was apparently the main limiting factor of the walking activity and forced the group to rest in the shade. The amount of time spent walking differed between cold, windy days (98%) and hot days (38%) (Kemp and Kemp, 1980).

Why study the Southern Ground Hornbill?

Ground hornbills are among Africa's most recognisable birds, exhibiting a large body size, a vibrant red throat colouration and striking black plumage (Kemp 2000; Trail 2007). The species holds ecological importance, and their utilisation of extensive home ranges, makes them indicators of environmental degradation and therefore valuable bio-indicators of environmental health (Kemp 1995; Trail 2007). Ground hornbills also hold cultural value, and are important resources for indigenous people, as food or as sources such as the use of their feathers, beaks and other parts used in cultural activities (Kemp 2000; Trail 2007).

The conservation status of the ground hornbill is formally listed as 'Vulnerable to Extinction' on the IUCN Red List (IUCN. 2012a, b; Cooper and Jordon 2013; Zoghby 2015; Taylor and Kemp, 2015a, b; IUCN 2019) in Africa generally but is considered endangered in both South Africa and Namibia (Theron 2011; Cooper and Jordon 2013; Zoghby 2015; Taylor and Kemp, 2015a, b). Although the ground hornbill is a nationally protected species in South Africa, its population numbers continue to decline (Theron 2011; Cooper and Jordon 2013; Zoghby 2015; Taylor and Kemp, 2015a, b). The principle threats to the ground hornbill are anthropogenic activities, which include habitat loss (MacDonald 1983; Vernon 1986; Kemp

1987; Morrison *et al.* 2007), the removal of nesting sites (i.e. large trees; Kemp and Kemp 1980; Morrison *et al.* 2007; Kemp 2017), direct and secondary poisoning (Kemp 2000; Morrison *et al.* 2007), exploitation for cultural purposes (Hockley and Archer 1966; Vernon 1986; Derwent and Mander 1997; Morrison *et al.* 2007) and persecution by farmers as a result of destruction of property (e.g. breaking windows; Forsberg 1994; Vernon and Herremans 1997; Morrison *et al.* 2007). Additional challenges that increase the vulnerability of ground hornbills are their long-life spans, requirements of large territories sizes, slow maturity and low reproductive success. These challenges influence their ability to adapt to and recover from environmental changes and threats, ultimately hindering their survival (Theron 2011; Cooper and Jordon 2013; Zoghby 2015; Kemp 2017).

Gap in our knowledge

As described above, two eggs are usually laid which hatch asynchronously, with the second-hatched chick usually dying within 3 weeks after hatching (Kemp 2005). This 'insurance policy' of having a second egg that is usually discarded has provided a valuable opportunity to conservationists. The second-hatched eggs, that would otherwise be discarded, are harvested and the chicks are captive-reared for the later reintroduction into areas which allow for the re-establishment of sustainable groups (Theron 2011; Cooper and Jordon 2013; Zoghby 2015; Taylor and Kemp, 2015 a, b).

Reintroduction projects have increased considerably over the years and have been a sustainable conservation mechanism for many species since the 1970s (Seddon *et al.* 2007). However, on closer observation of reintroductions, in particular bird reintroductions and translocations, it is evident that a large number of cases were unsuccessful (Theron 2011; Cooper and Jordon 2013; Zoghby 2015; Taylor and Kemp, 2015a, b). Reintroduction failures are the results of high costs, planning and logistical difficulties and, in many cases, a shortage of biological and ecological knowledge of both animal and habitat (Kleiman 1989; Seddon *et al.* 2007). Adequate knowledge of a species and its' habitat requirements need to be incorporated into planning for reintroductions (IUCN 2012a, b).

There have been many studies done on the biology (Kemp and Kemp 1980), breeding behaviour (Kemp and Kemp 1980; Theron 2011) as well as the general behaviour of the ground hornbill (Cooper and Jordan 2013) in free-living populations. This research, together with education, awareness campaigns, harvesting and hand rearing of second-hatched chicks,

as well as captive breeding programmes, have all been implemented to aid in the conservation of ground hornbills (Zoghby 2015). However, research of captive reared individuals is required to assess the suitability of individuals for breeding and potential future release. Only one study, that by Cooper and Jordan (2013), has considered the behaviour of captive ground hornbills. Yet, even though they studied the time-activity budgets in captive ground hornbills, they did not study their individual behaviour. Therefore, nothing is known about whether they have personalities and behavioural syndromes. Such knowledge of the behaviour of individuals and how it differs in different contexts could be beneficial for general captive handling and husbandry as well as for future reintroductions, by identifying suitable individuals to form pairs and social groups.

Aims, objectives and predictions

The aim of my study was to investigate the behaviour of captive ground hornbills housed in four institutions, representing six populations, in South Africa. These captive ground hornbills were captive hatched or wild caught birds, housed in pairs or small flocks. Specifically, I investigated whether the ground hornbills had personalities and behavioural syndromes, and whether there were sex and institution related behavioural differences.

The composition of the groups (sex and age) was determined by the institutions prior to my study, limiting the selection of study individuals to groups of non-random individuals with existing relationships. Yet, these individuals form the stock for captive breeding programmes and future release, and their behaviour might provide conservationists with important information about the phenotypes of the available captive ground hornbills.

Since little is known about the behaviour of ground hornbills, to meet the aim of this study, I adopted a broad approach by documenting basic behaviour, and specifically tested for individual differences, as outlined in the objectives below.

Objective 1. To describe the broad behavioural categories of captive ground hornbills

Objective 2. To document the diurnal activity patterns of ground hornbills in a captive environment

- Free-living ground hornbills have a bimodal activity profile (Kemp and Kemp 1980). I predicted that the activity profile of the captive ground hornbill would be similar to that of their free-living counterparts, where their activity will increase after sunrise, decrease towards midday (the hottest time of the day), increase again in the cooler hours after midday and decrease after sunset.

Objective 3. To investigate the transactional (two-way social) interactions of captive ground hornbills

- The four captive populations in this study were already well established prior to my study. Therefore, I predicted that there would be a higher frequency of amicable behaviour than aggressive behaviour.

Objective 4. To assess the space use and exploratory behaviour of captive ground hornbills

- I predicted that the ground hornbill would spend the majority of their time in areas of the enclosure that have large perches or trees, nest boxes as well as feeding stations.

Objective 5. To describe the risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle.

- If the ground hornbills display personality, I predicted individuals and sexes would differ in their risk-taking behaviour in an institution where some individuals are bolder than others and one sex (male) tends to be bolder than the other.

Objective 6. To assess the occurrence of a behavioural syndrome in individuals in each captive ground hornbill flock

- Using the data from objectives 1-5, I tested whether behavioural syndrome exist in ground hornbills. I could not predict *a priori* whether they would show behavioural syndromes.

MATERIALS AND METHODS

Study subjects and housing

The study was conducted from March 2017 to September 2017; data collection stopped in September due to the onset of breeding which could have influenced the data. Study sites included three locations in Gauteng, namely Johannesburg Zoo, Lory Park Animal and Owl Sanctuary and Monte Casino Bird Gardens, and one location in the Western Cape, at Hout Bay World of Birds (Figure 2), South Africa.

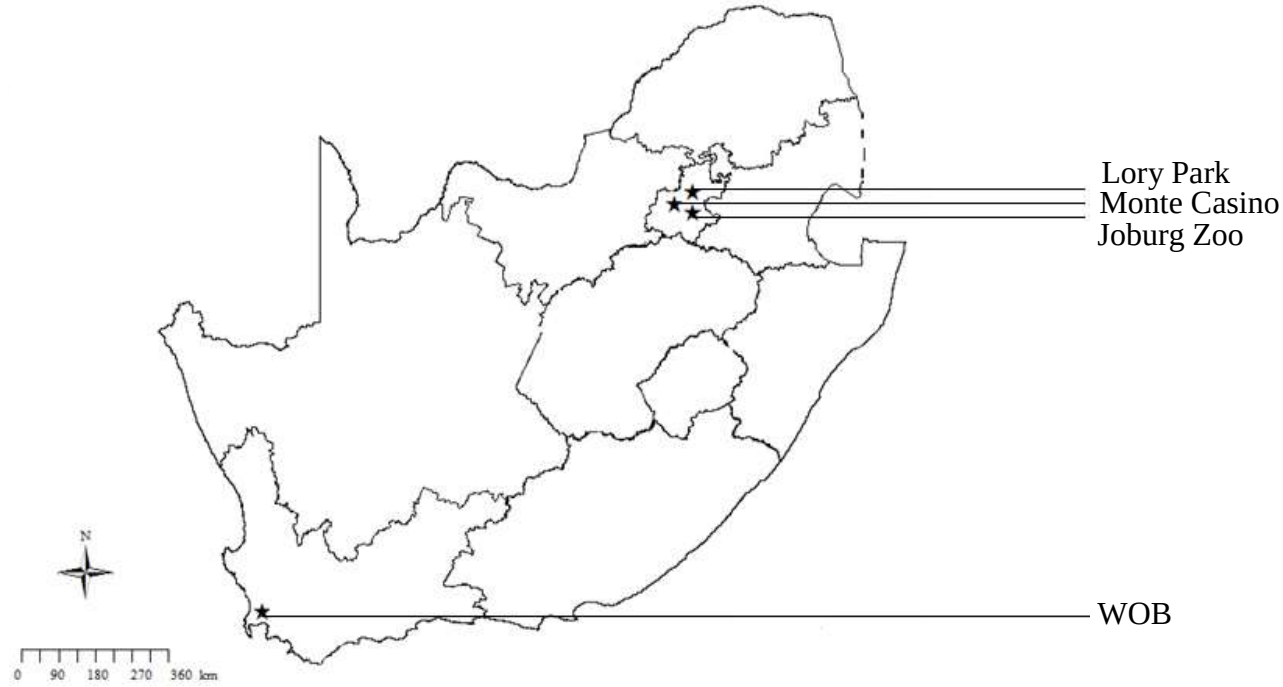


Figure 2: A map of South Africa showing the two provinces and four locations were studies were conducted. Lory Park: Lory Park Animal and Owl Sanctuary; Monte Casino: Monte Casino Bird Gardens; Joburg Zoo: The Johannesburg Zoo and WOB: Hout Bay World of Birds

In South Africa, there are a total of 13 certified captive institutions that house ground hornbills, namely Zaagkuilsdrift, Rhino and Lion Park, Loskop Dam, Umgeni River Bird Park, Johannesburg Zoo, Pretoria Zoo, Lory Park Zoo, Amazona, Ubhetyan O' Africa, Boscia Birds, World of Birds, Durban Zoo, and Hoedspruit Endangered Species Centre. Of the 13 institutions, only 6 of them are active participants in the Southern Ground Hornbill Action Group, and available for study. These four study sites were selected also because they housed a minimum of two ground hornbills, all with similar captive environments. These

were easily accessible for behavioural observations, and ensured my personal safety where data collection could take place from 06h00 and 18h00 (see below).

The Johannesburg Zoo

The Johannesburg Zoo (26.1666° S, 28.0376° E) is situated 6 km from the Johannesburg city centre, South Africa.

The Johannesburg Zoo housed two groups of ground hornbills, each consisting of three individuals, two males and one female in each (Table 1). The two enclosures were approximately 130 m apart and out of sight of one another. The first enclosure was located along a public visitor's path (hereafter referred to as the Joburg public enclosure). Even though the enclosure had exposure to the public on one side of the cage, there was a 1 metre gap between the path and the enclosure boundary fence, barricaded by a wooden picket fence (Figure 3). The second enclosure was situated inside a restricted public-access area (hereafter referred to as the Joburg hidden enclosure).

Table 1: Demographic data for the 18 Southern Ground Hornbills studied in four locations, three in Gauteng Province and one in the Western Cape Province.

Location	**Name**	**Sex**	**Age (Years)**	**Origin**	**Year of Capture/Hatching**
Joburg Hidden	Ntwanana_1995	Male	22	Wild caught	1995
Joburg Hidden	Nebo_2007	Male	10	Captive Bred	2007
Joburg Hidden	Tinto_2012	Female	5	Wild caught	2012
Joburg Public	Rhino_Road_2011	Male	6	Wild caught	2011
Joburg Public	Janovsky_2012	Male	5	Wild caught	2012
Joburg Public	Jasper_2013	Female	4	Wild caught	2013
Lory Park	Elvis_1992	Male	25	Wild caught	1992
Lory Park	Pricilla_2006	Female	11	Captive Bred	2006
Monte Casino	Hugo_1991	Male	26	Wild caught	1991
Monte Casino	Priscilla_1991	Female	26	Wild caught	1991
Monte Casino	Derek_1991	Male	26	Wild caught	1991
Monte Casino	Tsuwane_1991	Female	26	Wild caught	1991
World of Birds	T84	Male	17	Captive Bred	2001
World of Birds	T85	Female	17	Captive Bred	2001
World of Birds	Khumi_2013	Male	5	Captive Bred	2013
World of Birds	T129	Unknown	2	Captive Bred	2016
World of Birds	T134	Unknown	2	Captive Bred	2016
World of Birds	T147	Unknown	1	Captive Bred	2017

Joburg public enclosure

The public display enclosure was 31 × 12 × 6 m (length × breadth × height), with a total area of 2232 m^3, and comprised of 50 x 50 mm galvanised welded mesh perimeter fencing and a green nylon mesh shade cloth as the roof. To avoid any risk of the ground hornbills escaping, the enclosure had a built-in pre-entry enclosure (2 × 3 × 6 m), that consisted of the outside gate entering into it, and then a second gate entering into the main enclosure. Therefore, if one of the individuals tried to escape, they would have ended up in the small entrance enclosure and not outside with the public. The public display enclosure was situated between a pair of blue cranes *Anthropoides paradiseus* and a pair of saddle-billed stalks *Ephippiorhynchus senegalensis*. Each neighbouring enclosure shared a common boundary fence, and therefore direct interactions were possible.

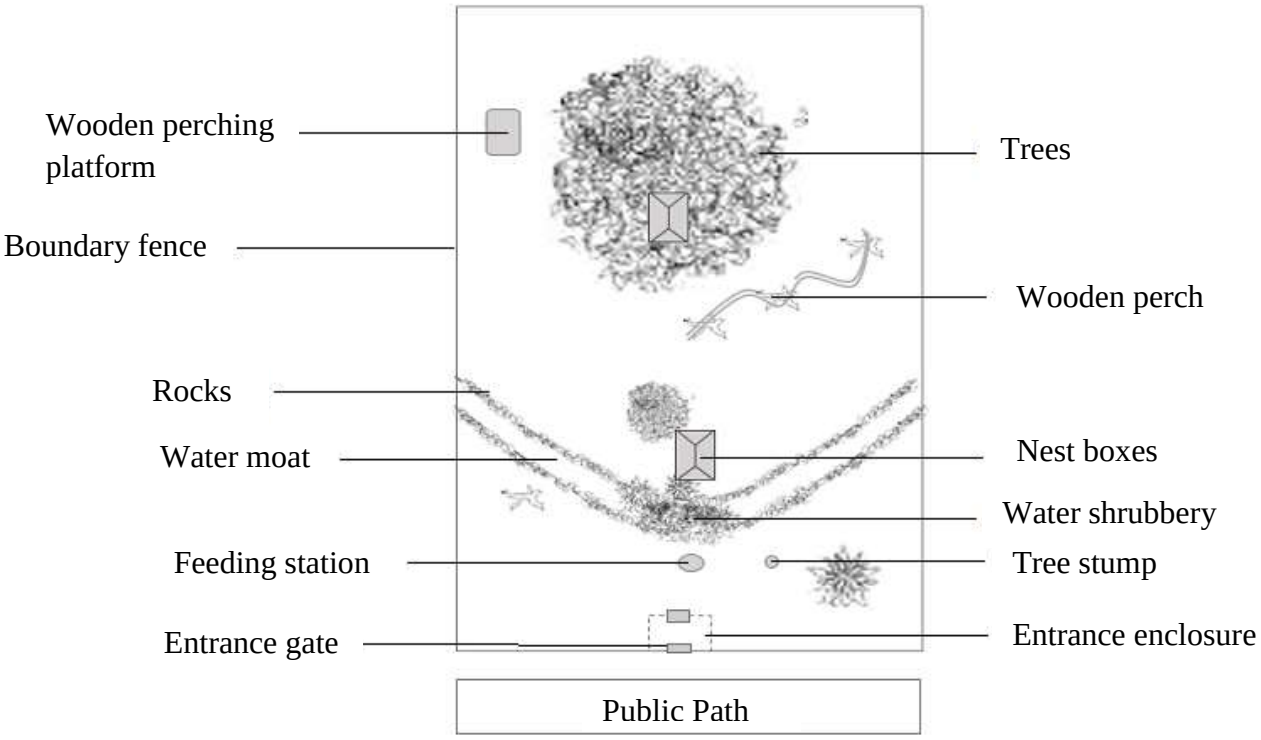


Figure 3: An aerial depiction of the Johannesburg Zoo Public display enclosure of Southern Ground Hornbill. Not drawn to scale.

The vegetation in the enclosure consisted of a large mature pin oak tree *Quercus palustris*, Sasanqua Camellia shrubs *Camellia sasanqua*, Spanish bayonet trees *Yucca aloifolia*, and a Bushwillow tree *Combretum* sp. As a consequence of the vegetation, there were large sections of the enclosure that had constant sun or shade, and other areas of the enclosure that had sun in certain parts of the day, although the green shade cloth roof allowed for a small amount of protection from the sun. Two nest boxes were positioned in the enclosure. One was a large dog kennel (81 × 102 × 98 cm), positioned in the large tree, situated in the upper back right section of the enclosure. The second, smaller nest box was a hollowed-out tree stump (diameter x height: 67 x 106 cm), positioned on a tall thick tree stump, situated in the upper front centre section on the enclosure (Figure 3). The enclosure also contained a large number of sedimentary rocks and 3 large perches made of wooden planks/platforms and poles and branches.

The composition of the enclosure floor consisted mainly of soft soil, and grass (family *Gramineae*). The enclosure had an artificial water moat that ran through the enclosure in a 'V shape' that was lined with water reeds (family *Poaceae*). There was one feeding point, which was a small tree stump (diameter x height: 40 x 20 cm), situated in the front centre of the enclosure. The ground hornbills were fed once a day at approximately 10h00. On Monday, Wednesday and Friday they were either fed 2kg of Guinea pigs (family *Caviidae*) or 2kg mice and one cup of NutriBird H16 pellets (balanced complete maintenance food for hornbills and other large fruit-eating birds). On Tuesday, Thursday, Saturday and Sunday, they were fed 2kg day old chicks. A combination of boiled eggs, an assortment of cut fruit, mealworms and crickets were added to the diet daily. A supplement of 3 scoops of Feli-Vit (essential amino acid taurine plus vitamins and minerals) was given to the ground hornbills daily. Water was provided *ad libitum* in a concrete bowl near the entrance as well as fresh water in the little water moat.

Joburg hidden enclosure

The hidden display enclosure was 24 × 6 × 6 m, and had a total area of 864 m^3. The perimeter fencing was the same as the public display enclosure and comprised of a galvanised welded mesh (50 x 50 mm). The enclosure also had a green nylon mesh shade cloth for the roof. The hidden display enclosure, like the public display enclosure, had a built-in pre-entry enclosure (0.6 × 1.5 × 6 m), and comprised of a different galvanised welded mesh (length × breadth: 25 x 50 mm) fence to the main enclosure (Figure 4).

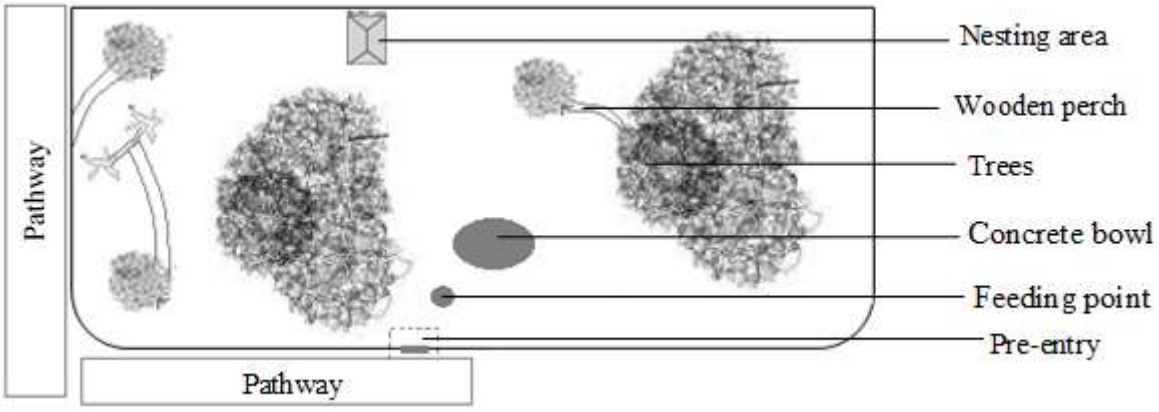


Figure 4: An aerial drawing of the Johannesburg Zoo Hidden display enclosure of Southern Ground Hornbill showing the layout of the plants, nest boxes and perching areas. Not drawn to scale.

The enclosure contained a paper-bark thorn tree *Acacia sieberiana* and a large common cabbage tree *Cussonia spicata.* These two large shady trees and the green shade cloth roof provided shade for the birds. There was no nest box available for the ground hornbills, and instead a small section of the cage that had waterproof roofing, situated in the back centre section of the enclosure, served as shelter. The enclosure contained 3 large perches made of wooden poles and branches.

The composition of the enclosure floor consisted mainly of soft soil, large sedimentary rocks and sparse grass patches (family *Gramineae*). There was one feeding point, which was a small rock (diameter: 40 cm), situated in the front centre of the enclosure. The ground hornbills were fed once a day at approximately 10h00, with a combination of day-old dead chicks, mice, and an assortment of cut fruit, mealworms and crickets. Water was provided *ad libitum* in a concrete cylinder bowl located near the entrance and feeding station. Enrichments (box of leaves or plastic bottles) were placed in the enclosure on random unscheduled days.

There was no general public access to the hidden display enclosure and only staff and a selection of visitors were able to interact with the ground hornbills. The enclosure had no adjacent enclosures, and therefore no direct interactions with other species. Approximately three metres in front of the enclosure was a concrete building which housed parrots *Cacatua* sp. and owls *Tyto* sp. and *Otus* sp., and to the left of the enclosure, about 2 metres away, was an enclosure that contained a blue crane *Anthropoides paradiseus*.

Lory Park Animal and Owl Sanctuary

Lory Park Animal and Owl Sanctuary (hereafter referred to Lory Park; 26.0091° S, 28.1527° E) is situated 30 km north of the Johannesburg city centre, in Midrand, South Africa. Lory Park housed one ground hornbill group, consisting of a male and a female (Table 1). The enclosure (9 x 4.6 x 6 m) had a total area of 324 m^3. Both the boundary fence and roof were constructed of 25 x 50 mm galvanised welded mesh and a blue fibre glass panel (length × breadth: 3 x 4.6 m) covered a portion of the roof for shelter from rain and sun (Figure 5). The pre-entry enclosure was situated at the back of the enclosure in a section restricted to zoo staff.

The composition of the enclosure floor consisted mainly of soft soil, sedimentary rocks, grass (family *Gramineae*), wild strawberries *Fragaria vesca* and woodrush *Luzula sylvatica*. A large wooden perching platform (length × breadth: 2 x 4.6 m) covered a portion of the back section of the enclosure which included the nest box and the feeding station (see stippled in Figure 5). There was one wooden nest box (1 × 1 × 2.5 m) situated in the lower back left section of the enclosure. In total, the enclosure had 8 perches made of branches and poles available for the ground hornbills.

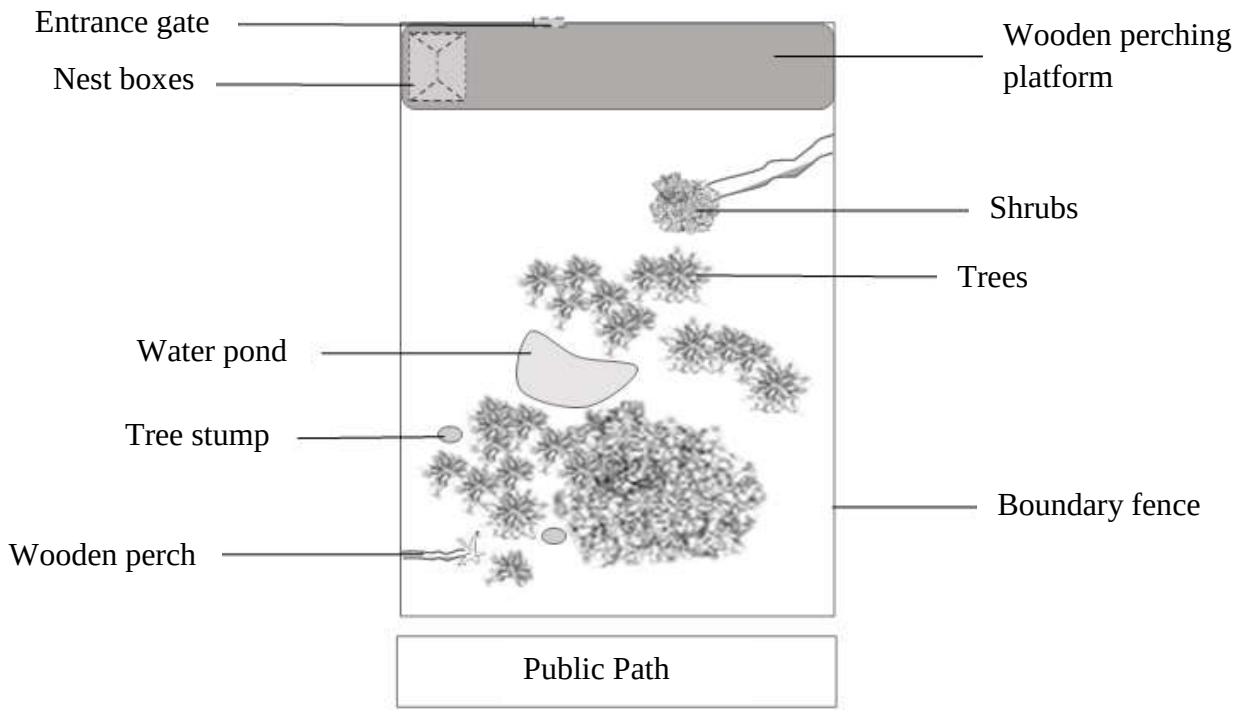


Figure 5: An aerial drawing of the Lory Park Southern Ground Hornbill enclosure showing the layout of the plants, nest boxes and perching areas. The entrance gate and nest box are stippled to show that they were positioned underneath a large wooden perching platform. Not drawn to scale.

The enclosure had an artificial water pond (diameter: 1m) that was lined with water reeds and woodrush. There was one feeding point, which was a plastic tray (diameter: 30 cm), situated in the back centre of the enclosure. The ground hornbills were fed twice a day, 7 days a week, before 8:00 and after 15:00. Their meals consisted of day-old chicks, soaked dog pellets, super worms and crickets. Water was provided *ad libitum* in the water pond.

The ground hornbill enclosure was located along a public visitor's path. However, there was a 1 metre gap between the path and the enclosure boundary fence, barricaded by a green metal picket fence which reduced the amount of direct interactions with the public. The ground hornbill enclosure was situated between a pair of African harrier-hawks *Polyboroides typus* and an Andean condor *Vultur gryphus* on one side, a pair of African fish eagles *Haliaeetus vocifer* on the other side, each neighbouring enclosure shared a common boundary fence, and therefore direct interactions were possible. A pair of Lar gibbons *Hylobates lar* was situated on the third side, three metres away across the public path.

Monte Casino Bird Gardens

Monte Casino Bird Gardens (hereafter referred to Monte Casino; 26.0239° S, 28.0110° E) is located 33 km north west of Johannesburg, in Fourways, South Africa.

Monte Casino housed two ground hornbill groups, each consisting of two individuals, one male and one female (Table 1). Both enclosures were situated inside a restricted public-access fenced off area, approximately 5 m apart, and were hidden away from the public. Each enclosure was 7.95 x 4.95 x 3.95 m, with a total area of 155.4 m^3. The enclosures were constructed of galvanised welded mesh (25 x 50 mm) fence. A brown concrete tiled roof (length × breadth: 3 x 4.6 m^2) covered approximately a quarter of the enclosure, sheltering the individuals from rain and sun (Figure 6). A black nylon mesh shade cloth covered each of the long sides of the boundary fence to prevent any visual contact between the two groups.

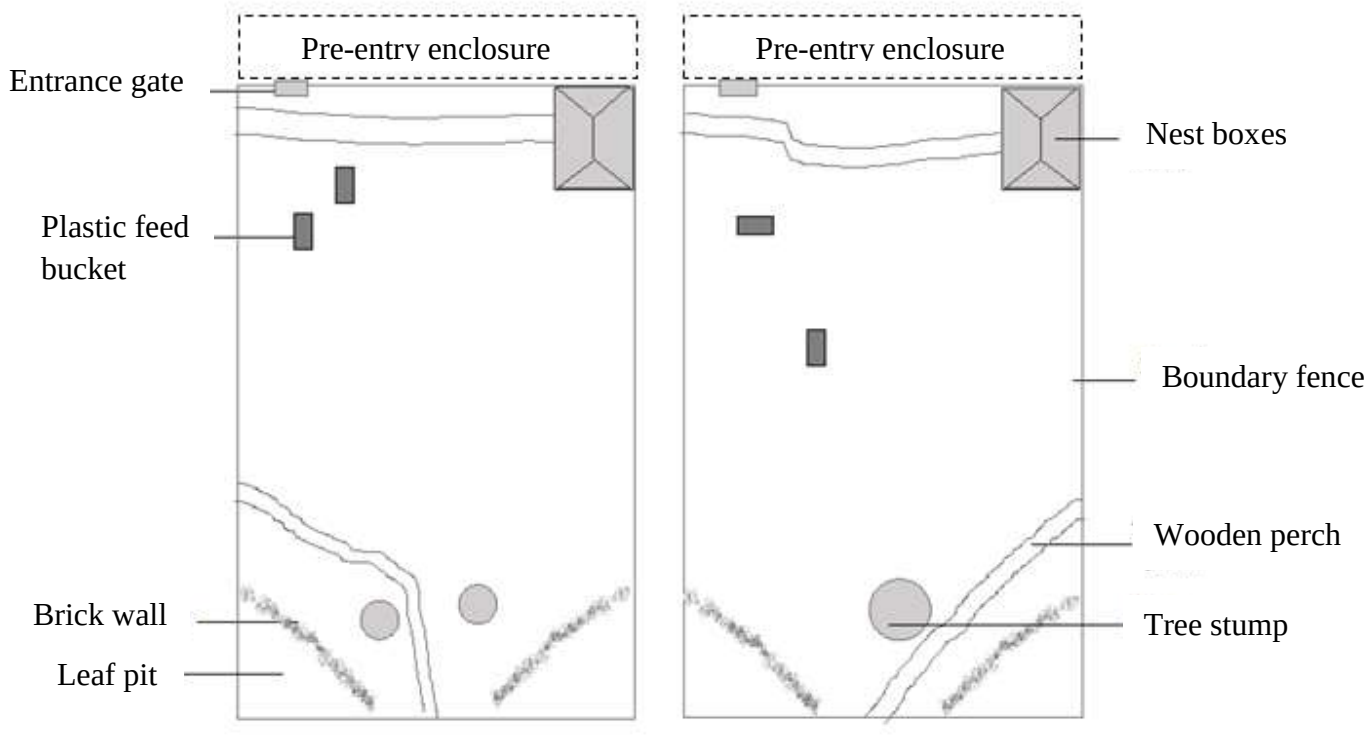


Figure 6: An aerial drawing of the Monte Casino Bird Park Left and Right enclosures housing Southern Ground Hornbill, showing the layout of the nest boxes and perching areas. Not drawn to scale.

The floor of each enclosure consisted of a combination of concrete, pebbles, sparse patches of grass (family *Gramineae*), and soft soil. There was no other vegetation present in each of the enclosures. Each enclosure had 2 large perching poles, one in the front section of the cage and the other in the back section of the cage, positioned under the covered roof of the cage. All 4 perches were positioned 280 cm above ground. There were two leaf pits in each corner (defined by a border of bricks) of the enclosure, in which tree branches and leaves were provided for enrichment as well as for nesting material. In each enclosure, a wooden dog kennel (91 x 61 x 72 cm), suspended 280 cm above the ground, was provided as a nest box (Figure 6).

There was one feeding point, which was a plastic feeding bucket (46 x 31 x 20 cm), situated on the ground in the back of the enclosure. Each pair of ground hornbills was fed 10 x day old chicks, an ox heart, 100g soaked dog pellets (NutriBird H16 pellets when in stock), an assortment of cut fruit, and a boiled egg in the mornings three times a week. On the other four days, they were fed 10 (a day old) chicks and 4 mice in the afternoon. Water was provided *ad libitum* in a plastic feeding bucket (46 x 31 x 20 cm), situated on the ground in the back of the enclosure.

The left enclosure was situated between a flock of Nicobar pigeons *Caloenas nicobarica* and an empty enclosure. The empty enclosure (7.95 x 4.95 x 3.95 m) that separated the two ground hornbill pairs, was used to house the ground hornbills when their enclosure was cleaned. This ensured that the keepers were not harmed by the birds. During cleaning, the gates to the empty enclosure was opened, and one pair of individuals was ushered into the vacant enclosure, the gates were then closed and the keeper was able to clean the original enclosure. At this time, there was only a single boundary fence separating the two pairs and therefore direct interactions were possible.

Hout Bay World of Birds

The Hout Bay World of Birds (hereafter referred to WOB), 34.0168° S, 18.3620° E) is located in Hout Bay 21 km from Cape Town. Hout Bay.

WOB housed six ground hornbills in one group, consisting of two males and one female and three juveniles of unknown sex (Table 1). The enclosure was 25 × 12 × 7 m, with a total area of 2100 m^3, which was constructed of galvanised welded mesh (50 x 50 mm) fence, which was the same material used for the roof. A black nylon mesh shade cloth was present on three of the boundary fences. The enclosure had a built-in pre-entry enclosure (2 × 3 × 6 m).

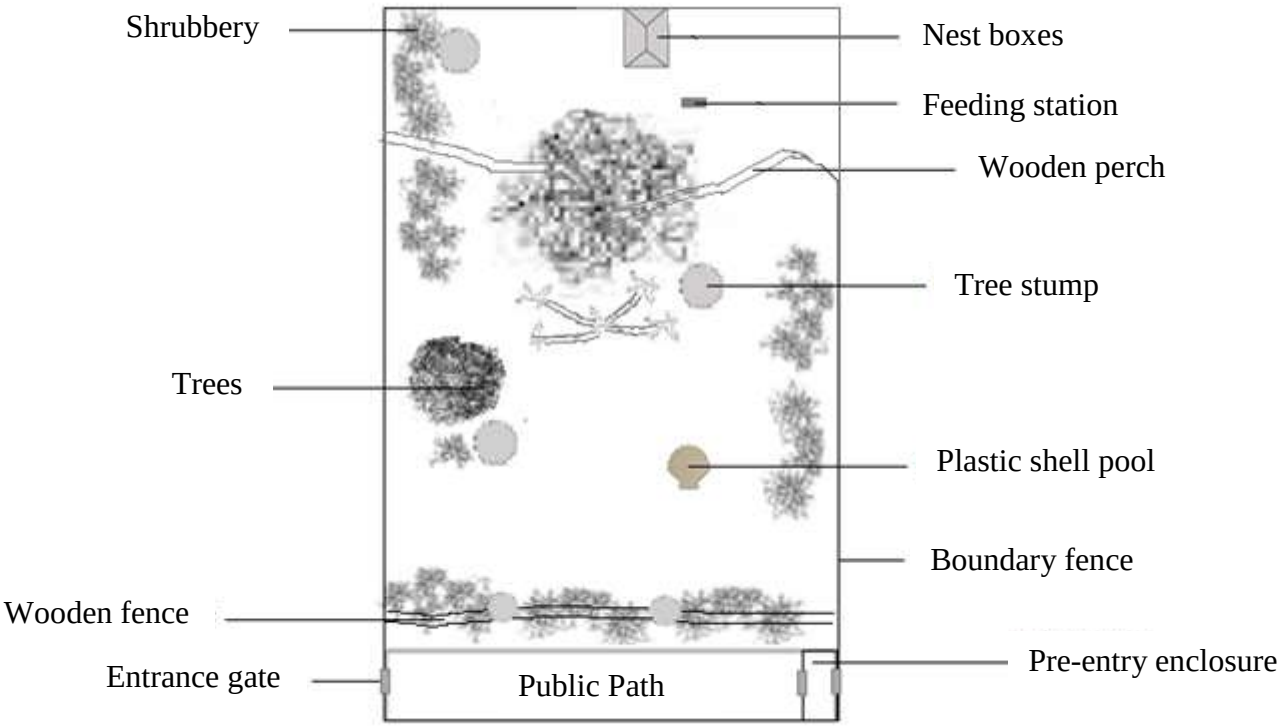


Figure 7. An aerial drawing of the Hout Bay World of Birds Southern Ground Hornbill enclosures showing the layout of the nest boxes and perching areas. Not drawn to scale.

The enclosure contained two large trees, namely a Beef-Wood tree *Casuarina cunninghamiana*, and a Yucca tree *Yucca Brevifolia*. As a consequence of the vegetation, there were large sections of the enclosure that had shady areas.

A large shady tree (Beef-Wood) in the back right section of the enclosure supported one of the two nest boxes in the enclosure. One wooden nest box (81 × 102 × 98 cm) was positioned in the back right section of the enclosure. The second, smaller nest box was a hollowed-out tree stump (diameter x height; 67 x 106 cm). The enclosure also contained a large number of sedimentary rocks and 5 large perches made of wooden planks, poles and branches.

The composition of the enclosure floor consisted mainly of soft soil and grass (family *Gramineae*). There was one feeding point, which comprised of two plastic trays (diameter; 30.48 cm), situated in the back right section of the enclosure. The ground hornbills were fed twice a day at approximately 09h00 and 16h00, with a combination of day old chicks, chicken necks, chicken mince, mice and soaked dog pellets. Water was provided *ad libitum* in a yellow plastic Addis 1 x 10 Litre Clam Pool.

The ground hornbill enclosure was situated between enclosures that housed Black-crowned night heron *Nycticorax*, black crowned cranes *Balearica pavonina*; American coot, *Fulica americana* and Northern Bald Ibis, *Geronticus eremita*, on one side and a Spotted Eagle Owl, *Bubo africanus* on the other. Each neighbouring enclosure shared a common boundary fence, and therefore direct interactions were possible. The public visitor's path was situated inside the cage, where visitors had complete access into the enclosure. Therefore, direct interactions between the visitors and the ground hornbills were possible.

Protocol and Design

The broad behavioural categories of captive ground hornbills

Written transcriptions

This experiment was done separately to the general behaviour, sociability and space use observations. I allocated one hour (full 60 minutes) of time for each enclosure (6 hours in total), where I observed the individuals. I spent 6 hours recording. Once I had descriptions of behaviours for the 18 birds in the 6 populations, I edited and condensed my descriptions into nine functional categories (See results).

Video recordings

I also recorded video footage of the behaviour ofground hornbills at the WOB location. Because I was permitted to enter and conduct observations inside the enclosure, there was no visual hindrance of the fence as in the other locations.

I filmed the behaviour of the birds after collecting general behaviours (mentioned above) which allowed the birds to habituate to my presence. The videoing was done separately to the general behaviour observations as there was no time to video and capture accurate behavioural data simultaneously. I sat inside the enclosure at a safe distance (same position as mentioned above in the general behaviour) and video recorded the behaviours of the birds until all behaviours had been displayed.

Digital recordings of behaviours (from the WOB location) were used to create a video catalogue, representing an important repository for storing behavioural acts of the ground hornbills. Importantly, since the definitions of behaviours are sometimes unclear, such video footage could help standardise the behavioural sampling protocols and thus provide an invaluable resource for future ground hornbill researchers and conservationists.

Diurnal activity patterns

I conducted direct behavioural observations of individual ground hornbills. Each individual in each group per location was observed for a total of 24 hours per month. Such data collection provided data for individuals in a short time period.

At the Johannesburg Zoo, Lory Park and Monte Casino locations, I conducted observations from a fixed position 5 m outside of the enclosures using a pair of Bynolyt Runner II 7x50 binoculars, ensuring a clear view of the hornbills. The WOB ground hornbills were habituated to human presence, and therefore I was permitted to enter and conduct observations inside the enclosure. I sat inside the enclosure with my back against the boundary fence, on the public path, at a safe distance from the nest box, feeding station and perches with only a small wooden picket fence separating me from the birds.

At the beginning of the experiment, I waited 10 minutes for the ground hornbills to become habituated to my presence. Thereafter, using direct observation, I recorded the frequency of behaviours of individuals every 2 minutes using focal sampling (Altmann 1974, Martin and Bateson, 1993). The behaviours were recorded according to the categories listed in Table 2 (Page 50). In addition, I recorded the location of each individual in different sections of the enclosure (objective 4: space use; see below), every 2 minutes.

Each individual was observed for a 12-hour period from 06h00 and 18h00, three to five times a week, lasting between 6 to 8 hours per day. To capture a full 12-hour activity period, each individual was observed for the 12-hour daily activity, with behaviours recorded from 06h00 and 18h00. In order to achieve the full 12 hour observation, each individual was observed three to five times a week, lasting between 6 to 8 hours per day. This ensured that behaviours were recorded for the 12 daylight hours. After 12 hours of recording per individual, I generated a cumulative frequency curve (per individual), representing the frequency accumulation of behaviour per individual in a group, in order to establish whether the sampling period was appropriate and adequate for obtaining all the behaviours in Table 2.

Sociability

Here, I investigated the interactions of the ground hornbills with one another. These data were collected simultaneously with the general behaviour observations (i.e. every 2 minutes during sampling). I used a socio-metric matrix analyses in MatMan version 1.0 for Windows (Noldus Information Technology 2013) to assess whether the individuals at each location differed in the probability of positive/neutral to negative interactions instigated and received by other individuals in the enclosure. The matrices were summed from the combined social data per individual and per location. These summed matrices were used to calculate adjusted residuals.

Space use

Space used was observed concurrently with the general behaviour and sociability observations mentioned above (i.e. every 2 min). Since the number of individuals was greater at WOB, space use was not assessed at WOB due to time constraints.

The space use of individuals was recorded on a three dimensional map of the enclosure, in which 12 approximately equally sized zones were demarcated (Figure 8). The zones were equally mapped out by me walking the length and breadth of the enclosure and measuring the enclosures dimensions and equally dividing the shorter breadth by two and the longer length by three (Figure 8), creating 6 zones confirmed by landmarks like a fence pole or tree. The six ground level zones were the same for the six upper zones.

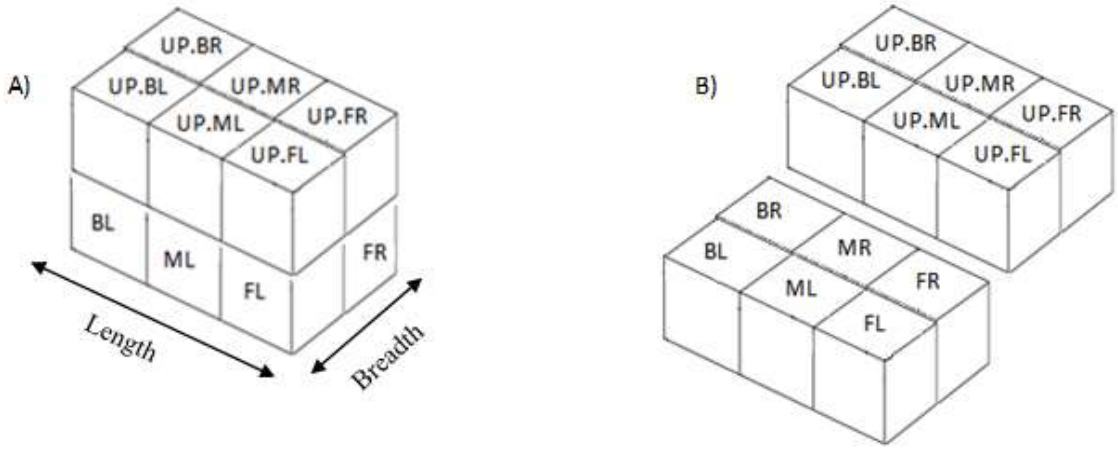


Figure 8: A diagrammatic representation of the A) 12 zones (six upper zones and six ground level zones) for the ground hornbill enclosures at the Johannesburg Zoo, Lory Park and Monte Casino Bird Gardens, and B) longitudinal division through the diagram in (A) to better illustrate the 12 zones. The names and abbreviations of the of the 12 zones (Six upper zones and six ground level zones) were; back left- BL; back right- BR; middle left- ML; middle right- MR; front left- FL; front right- FR; Upper Back Left- UP.BL; Upper back right- UP.BR; upper middle left- UP.ML; upper middle right- UP.MR; upper front left- UP.FL; upper front right- UP.FR.

Of the 5 enclosures, four of them were regular rectangular shaped (Joburg hidden display, Lory Park and Monte Casino) and the zones were identical in size. However, in the irregular Joburg zoo hidden display, the zone demarcation was different, and the zones were divided as equally as possible, although some zones had rounded corners, being slightly smaller than others. Each zone was similar in size within each enclosure but differed in size among the different enclosures.

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle

Here, I used two well-known personality tests in the literature, namely startle tests and novel object tests (Wilson *et al.* 1993; Torgerson-White and Bennett 2014; Yuen *et al.* 2016). For both the startle and novel object tests (below), I could not assess the behaviour of individuals in isolation, because none of the institutions permitted me to capture and isolate individuals, which was deemed stressful for the birds.

Experiment 1: Startle test

Each group was assessed once every 24 hours for three replicates. Replicate is defined as the same startle test done again in exactly the same way. To ensure the health and wellbeing of the ground hornbills, only one test per day was conducted and lasted a maximum of 10 minutes per test.

At the start of each experiment, a digital camcorder (Sony DCR-SX44) was mounted in a fixed position in front of the cage, about half a metre above the ground, and placed onto auto-focus mode. I moved to an out of sight position about 8 metres away from the ground hornbill enclosures. Each population was then video-taped for a period of 5 minutes to confirm that the birds had habituated to the presence of the camera (i.e. they resumed their previous activity). After the 5 minute habituation period, a startle stimulus was produced by me letting off a loud siren sound (80 decibels) from the portable hand held siren (Topline International: Walk Easy Personal Emergency Alarm) for 15 seconds from an out of sight position outside the enclosure (video-taping continued during this period).

I used a portable hand held siren due to the fact that it was easily obtainable, it did not produce a sound that could be previously heard by the ground hornbills, and it was loud enough to make an effective startle sound.

Video recording was continued for 5 minutes after the startle stimuli. From the video recordings, the latency (in seconds) it took for each individual in a group to resume its normal activity (one of the behaviours mentioned in Table 2) was recorded.

Experiment 2: Novelty test

The novel object tests were conducted on a separate day to the startle tests. Each novel object experiment lasted 40 minutes per test session. Like the startle tests, each individual within each group was assessed once every two days (24 hours) for three replicates.

As for startle tests, prior to the experiment, a digital camcorder (Sony, DCR-SX44) was mounted in a fixed position in front of the cage. Each group was then video-taped for a period of 5 min to habituate to the camera. After the 5 min camera habituation period. I was assisted by a zoo keeper. I entered the enclosure at the Johannesburg zoo and WOB and placed a large metal garden chair (102 cm x 45 cm; Figure 9) directly in front of the mounted camera (video-taping continued during this period). At Lory Park and Monte Casino, only the zoo keeper was permitted to enter the enclosure. We then immediately vacated the enclosure and moved to a position out of sight of the hornbills. Video recording was continued for a further 30 minutes. Once the session was completed, the chair was removed from the enclosure.

From the video footage, I recorded the latency (in seconds) of individuals to approach the novel object (within a 50 cm proximity), and the time spent interacting with the object. In the cases where an individual did not approach the novel object, the latency to approach the novel object was scored as the maximum time of 30 minutes and the time spent interacting with the object was scored as zero.



Figure 9: The large metal garden chair used in novelty object tests for ground hornbills

The behavioural syndrome in captive ground hornbills

All subjects were tested and observed individually in 3 experiments (Objectives 2; 3 and 5), namely the general behaviour observations, the sociability observations, and the startle and the novel object tests. The data that were collected from each of those tests were then correlated.

Data analyses

All statistical analyses were conducted in R Studio (Version 3.3.0; R Development Core Team 2006) and GraphPad InStat 3 (Version 3.06; www.graphpad.com). The entire data set was screened for normality using the Shapiro-Wilk normality test, and transformed. All tests were two-tailed with statistical significance accepted at $p \leq 0.05$.

The broad behavioural categories and diurnal activity patterns of captive ground hornbills

The data were square-root transformed to approximate normality. A linear model using lm function and Anova function in the car package was used to analyse the influence of location and sex (fixed factors) on each behaviour (i.e. locomotion, feeding, interaction with item, social interaction, perching, lying down, vocalising, preening, and thermoregulation) separately (dependent factors) (Crawley 2007). The behaviours were pooled for all hours of sampling for each ground hornbill population because of relatively constant behaviour throughout the day and because hourly sampling was not statistically possible with the small sample sizes per institution. I used the *lsmeans* package to run a Tukey's HSD post hoc test to identify where significant differences occurred (Bates *et al.* 2015). To correct for the multiple comparisons of multi-dependent behaviours (i.e. the occurrence of one behaviour was dependent on occurrence of another behaviour), I adjusted P values using the Benjamini and Hochberg (1995) method for location and sex separately.

The transactional (two-way social) interactions of captive ground hornbills

For the analysis of the aggressive and amicable interactions that occurred between the individuals in each group, I analysed the frequency of amicable and aggressive interactions for each individual in each population. I then used a socio-metric matrix analysis in MatMan version 1.0 for Windows (Noldus Information Technology 1998) to assess whether the individuals at each location differed in the probability of positive/neutral to negative interactions instigated and received. The matrices were summed from the combined social data per individual and per location. These summed matrices were used to calculate adjusted residuals. Both positive and negative residuals were calculated and expressed according to a Z-distribution. Using these results, a table of positive and negative matrices were generated for each individual in each location. Location was analysed separately because enclosures were different shapes and sizes.

The space use and exploratory behaviour of captive ground hornbills

The space use of ground hornbills was analysed using a general linear model (GLM) Here, I considered the use of the different parts of the enclosure by individual ground hornbills. The effect of individuals (ID), zones, and the interaction between individuals and zones on the use of space was analysed. Location was analysed separately because enclosures were different shapes and sizes. Space use was assessed at all three locations in Gauteng Province, but not at the WOB in the Cape Province where recording the location of the large number of birds was challenging.

The space use data were summed up for each of the 12 zones (Table 4) for each individual in its enclosure. For each enclosure, the data were analysed to determine which sections of the cage were utilised more frequently than others, using a Generalised Linear Model with a Poisson error structure and log link function. The Individuals (ID) and the zones were fixed factors, and frequency of occurrence in each zone was the dependent variable. Location was analysed separately because enclosures were different shapes and sizes. Reference categories were selected using sequential entry to obtain Z statistics for each component. The Back Left (BL) zone was used (in each population) as the reference category for the zone effect, and Back Left (BL) Zone and the female individual (in each population) was used as the reference for the Zone-ID effect.

Using the frequency data, four quartiles were calculated per zone, for each individual per location, to generate a frequency of space use occurrence map. To calculate the quartiles for each individual, I first ordered the data from lowest to highest and calculated the overall median. The minimum (smallest number) was used as quartile Zero (Q0), the first quartile (Q1) was calculated as the middle number between the smallest number and the median of the data set. The second quartile (Q2) is the median of the data. The third quartile (Q3) is the value between the median and the highest value of the data set. The fourth quartile (Q4) is the maximum (largest number). These quartiles were colour coded to provide a visual representation of the use of the enclosure by individuals.

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle

Here, I compared the data in each variable (latency in seconds) among the institutions. For this, I square-root transformed the data. The transformed data were then analysed in a linear

mixed model (LMM) using the *lme4* package (Bates *et al.* 2015). In these analyses, sex, replicate number and location were the independent factors, time was the dependant factor and individuals were the random factors. Tukey post-hoc tests (*lsmeans* package) were used to identify specific trends when the analyses were significant at $\alpha \leq 0.05$.

Next, I scored the duration of time taken to return to normal behaviour (startle test), the duration of time taken to approach, as well as the duration of time spent interacting with the novel object (novel object test). I compared data for each variable between ground hornbills for the three replications in each enclosure using chi-squared contingency analysis. This test was appropriate because only one value per individual per replicate was recorded. I used a contribution to chi-squared analysis to assess individual variation in risk taking behaviours; this test compares the observed to expected outcome in each cell of a contingency table.

The behavioural syndrome in captive ground hornbills

To assess whether behaviours (frequency (number/counts displayed per (every 2 minute interval) correlated between feeding; perching; social interaction; vocalization; preening; lying down; locomotion; object interacting; thermoregulation, a Pearson's product-moment correlation coefficient was used using GraphPad InStat 3 (Version 3.06; www.graphpad.com). A significant correlation between several variables would indicated an association between them, and therefore suggest that a syndrome exists (Silber *et al.* in press). In addition to $\alpha \leq 0.05$, I only considered responses with R-values greater than 0.5 to form syndromes. Data were combined for all individuals in the study because of the low number (2-3 individuals) in five enclosures, which had low statistical power.

RESULTS

Data were collected for 18 ground hornbill individuals for analysis of their general activity, behavioural differences, sociability and space use differences. Nine behaviours were recorded.

The broad behavioural categories of captive ground hornbills

A total of 9 behaviours were recorded (Table 2) and described (below). I also assigned uncommon behaviours to an 'Other' category. Video links are provided for selected behaviours below.

Table 2. The behaviours recorded in the ground hornbill individuals at the four locations in Gauteng and the Western Cape provinces

Behaviour	**Description of behaviour**
Perching	A continuous period resting on an object above ground
Locomotion	Walking or running (never having both feet off the ground at once); and flying (typically 30 cm or more above the ground with broad open wings which are flapped up and down in a repetitive movement)
Interaction with item	Any physical contact between the beak and a non-food item (e.g. stone)
Lying down	A continuous period of resting on the ground (legs tucked underneath body and not visible)
Social interaction	• Positive/neutral interaction - allo-grooming/allo-preening, social play, allo-feeding, and neutral side-by-side perching, resting or lying down • Negative interaction – aggressive chasing, snatching food/object from another individual (negative interaction is usually associated with a vocalisation)
Preening	Grooming and cleaning feathers with the beak or foot
Feeding	Taking a food item in mouth and swallowing
Thermoregulation	Resting in the shade; wings held away from the body; opening of the bill; basking; huddling; rest in sunny areas
Vocalising	Sound produced from the mouth
Other	Any other behaviour displayed that did not fall into the above categories

1. Perching

Perching or roosting behaviour was noted when an individual rested on an object above ground. The ground hornbill flew up into a tree or perch, and rested in either a standing position (feet visible), or down across the branch so that its feet were not visible (often tucking its head between its wings). On many occasions, individuals roosted in close proximity to one another on the same tree or perch.



Picture 1: An example of perching behaviour.
Photo permission granted by Joel Ranjithkumar.

Perching: https://www.dropbox.com/s/q8yladdovd2cucv/1-Perching.mp4?dl=0

2. Locomotion

Locomotion was defined as any movement (forward or backward) from one point to another. The first form of locomotion was walking, which was a rather stiff rolling movement achieved by lifting and setting down each foot in turn; never having both feet off the ground at once. The second form of locomotion was running which differed to walking by having the gait with kinetic and gravitational potential energy, fluctuating in phase, unlike walking which fluctuates out of phase (Daley and Birn-Jeffery 2018).



Picture 2: An example of walking behaviour.
Photo permission granted by Johan Smalman.

Walking: https://www.dropbox.com/s/ecq9j8t1ivdn0en/2-%20Locomotion_Walking.mp4?dl=0

Running: https://www.dropbox.com/s/90kciz0aqhdpinv/2%20-%20Locomotion_Running.mp4?dl=0

Hopping or jumping were very uncommon, and, when expressed, were mostly used for movement over rocks and in trees.

Flying consisted of strong deep flaps of the broad wings with little gliding. Flight was usually within 1 m off the ground and was normally used to travel to the perches or tree branches.



Picture 3: An example of flying behaviour. Photo permission granted by Kathleen Vanoppen.

Flying: https://www.dropbox.com/s/hj8zcirouw32hjw/2-%20Locomotion_Flying.mp4?dl=0

3. Object Interaction

Item interaction was defined as any physical contact between the individual's beak and an object (e.g. stone, fence). Here, an individual approached an object, and touched it with its beak. On some occasions, the ground hornbill pecked at a solid object (e.g. tree, food bowl) and the item produced a loud sound.

Object Interaction: https://www.dropbox.com/s/oxz06v1zcrrqm9s/3%20-%20Object%20Interaction.mp4?dl=0

4. Lying Down

Lying down was recognised as a continuous period of resting on the ground (legs were not visible). The ground hornbill squatted down into a position so that its feet were not visible and on some occasions would tuck its head between the wings.

Lying Down: https://www.dropbox.com/s/j2fwdnhqsqgpooi/4%20-%20Lying%20Down.mp4?dl=0

5. Social Interaction

Social behaviour was defined as any interaction with another individual of the same species. Social interaction included social play, which consisted of either birds chasing one another on foot or in flight, probing and tugging at one another, or tug-of-war with an object held in the bill. Agonism was seen only once in the large 6 individual group at WOB, where the adult male attacked and dispersed the juveniles that had been playing in a social play.

Social interaction also included allopreening which was the act of one individual (mainly the male) preening another individual (mainly the female). Kemp and Kemp (1980) stated that allopreening is a sexually motivated behaviour and is a prelude to copulation. Allo-feeding interactions occurred when one (male or female) ground hornbill carried a food item in its bill and another individual (male or female) approached and was fed. On the rare occasion, the individual with the food responded with a head-up threat or turned away.



Picture 4: An example of social (allo-preening) behaviour.
Photo permission granted by Earnest Scribbler.

Social Interaction: https://www.dropbox.com/s/ls3h6gkl3s5me68/5%20-%20Social%20Interaction.mp4?dl=0

6. Preening

Preening was categorised as tidying and cleaning feathers with the beak or claw. Head scratching, face-wiping on the foot, bill cleaning on objects as well as by scratching, oiling, and nibbling at their feathers, were all behaviours that were recorded as preening behaviour.



Picture 5: An example of preening behaviour.
Photo permission granted by Varun Aditya.

Preening: https://www.dropbox.com/s/asbv3vqdi7s38s0/6%20-%20Preening.mp4?dl=0

7. Feeding

I considered feeding behaviour when a ground hornbill approached a food item, picked it up in its beak and threw its head backwards and then swallowed the food. Occasionally, when the food was large (e.g. a dead chick *Gallus domesticus*), the individual picked up the food, performed a kill bite head shake which would cause part of the chick to tear off. The ground hornbill then threw back its head and swallowed and then walked over to the rest of the chick



Picture 6: An example of feeding behaviour.
Photo permission granted by Varun Aditya.

and repeated the process. In some instances, one ground hornbill individual took food from another individual, either forcibly or by being offered the food item by the other individual.

Feeding: https://www.dropbox.com/s/au1nflp1wcrw8sc/7%20-%20Feeding.mp4?dl=0

8. Thermoregulation

Heat loss behaviour was observed when a ground hornbill opened its bill and, at the same time, held its wings away from its body to cool down. Another indication of heat loss behaviour was when the bird moved into the shade either on the floor or up into the shade of trees or perches. To gain heat, a ground hornbill lay down/basked in a sun exposed area of the enclosure.



Picture 7: An example of thermoregulatory behaviour.
Photo permission granted by Khadija Bham.

Thermoregulation: https://www.dropbox.com/s/jnywl4i50o7w52e/8%20-%20Thermoregulation.mp4?dl=0

9. Vocalisation

Vocalisation was defined as any sound produced from the throat. The sound normally consisted of a deep resonant four-note call, *uuh uuh uuuh-uuh.* The vocalisation behaviour was normally performed from a position on a perch or a tree branch, but was also performed while standing or walking on the ground, or (very uncommon) while flying. On some

occasions, the ground hornbill displayed a harsh nasal bray sound, which Kemp and Kemp (1980) state is usually uttered by chicks, immatures or the breeding females when taking food from another bird.

The diurnal activity patterns of captive ground hornbills

A total 360h of sampling was conducted (6 enclosures x 5 months x 12 h), resulting 10800 observations. The total frequencies for the behaviours of all 18 individuals in the populations were recorded and converted into percentages of total behaviours. Of the 9 behaviours recorded, perching (25.86%) was the most common behaviour.Less frequently observed behaviours were feeding (5.33%), thermoregulation (5.09%) and vocalising (4.87%) (Figure 10).

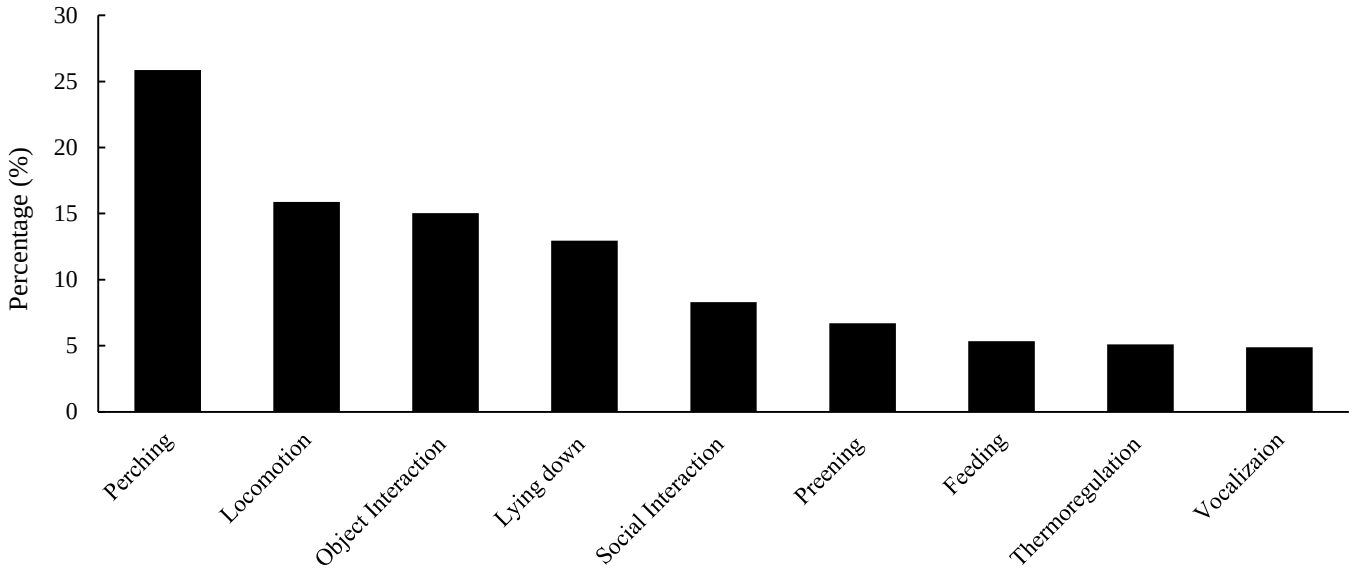


Figure 10: Percentage of time devoted to 9 behaviours by of 18 captive ground hornbills *Bucorvus leadbeateri* in Gauteng and the Western Cape provinces.

Activity (time-budget) profiles

The activities of the ground hornbills varied throughout the daylight hours. The comparisons of the activities in 12 hours (06:00 to 18:00) of the day were done for the three most common behaviours: perching, interaction with an object, and locomotion (Figure 11), for all ground hornbills in the study, since the number of ground hornbills sampled were small (the activity profile of each population separately is provided in Supplementary 1).

The graph types constructed are similar to those of Kemp and Kemp (1980), to permit comparisons between our studies. The frequency of perching was fairly constant throughout the day, but had a subtle binomial distribution where it decreased around midday, and then slowly rose towards later afternoon. The frequency of object interaction was lower in the first hour and in the last hour of sampling, and was constant during other times of the day. Locomotion was in the first and last hours of sampling and fluctuated through the day (Figure 11).

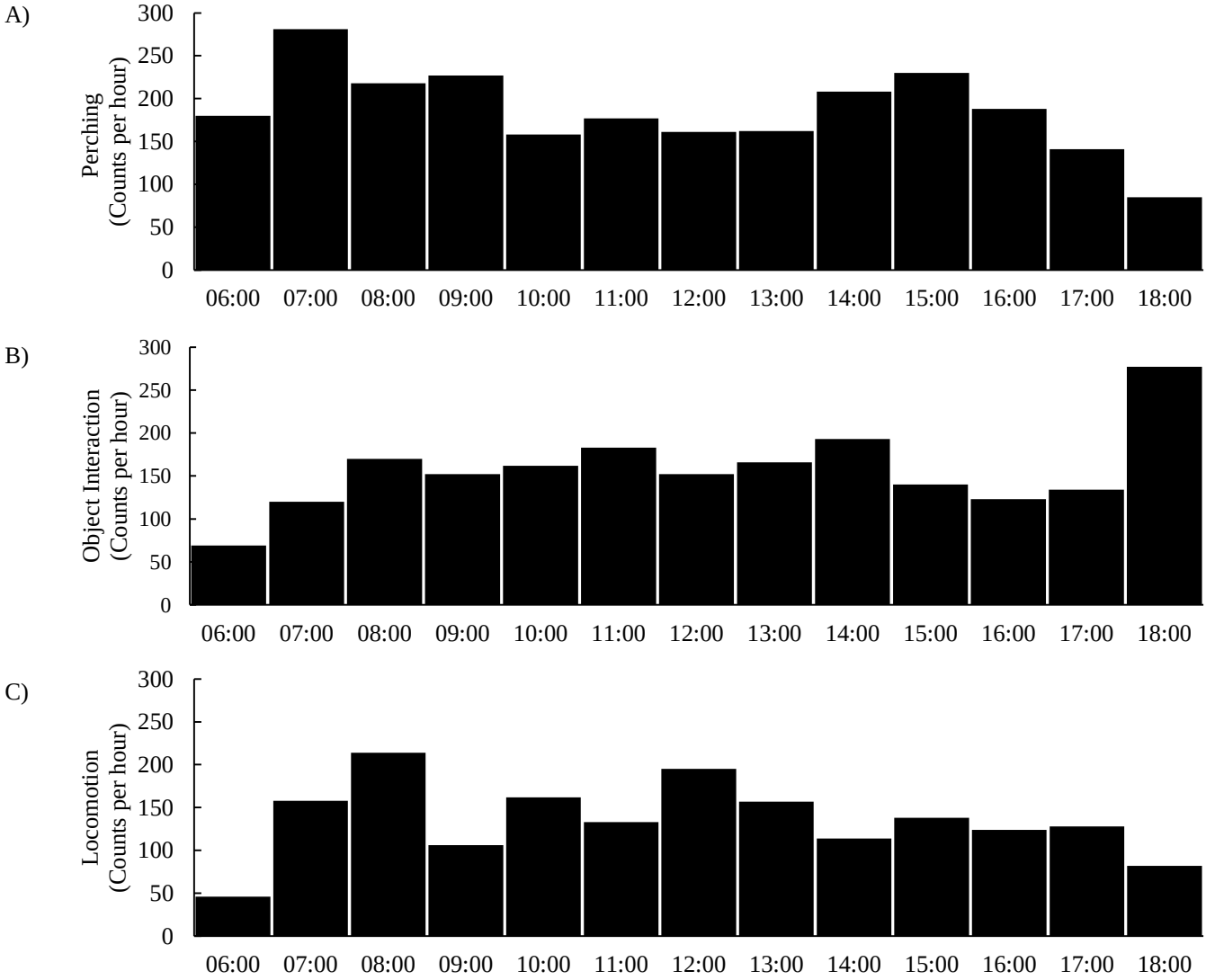


Figure 11: The 12 hour activity-time profile of A) perching, B) interaction with an object and C) locomotion in 18 captive ground hornbills. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Perching

Location was a significant predictor of perching behaviour ($F_{5, 11} = 8.61$; adjusted $p = 0.043$). The individuals in Joburg hidden enclosure perched significantly less than 3 of the 5 populations, namely the Lory Park individuals ($p = 0.036$), the Monte Casino Right enclosure ($p = 0.012$) and the Monte Casino Left enclosure ($p = 0.011$; Figure 12). The Joburg public display perched significantly less than 2 of the 5 populations, namely the Monte Casino Right enclosure ($p = 0.028$) and the Monte Casino Left enclosure ($p = 0.010$). The other institutions were similar and did not differ significantly in their perching behaviour ($p>0.05$). Sex was not a significant predictor of perching behaviour ($F_{1, 11} = 4.061$; adjusted $p = 0.073$).

Locomotion

Location was not a significant predictor of ground hornbill locomotion ($F_{5, 11} = 2.84$; adjusted $p = 0.135$). However, sex was a significant predictor of locomotion ($F_{1, 11} = 7.48$; adjusted $p = 0.031$). Females locomoted significantly less than males ($p = 0.024$).

Item Interactions

Neither location ($F_{5, 11} = 2.26$; adjusted $p = 0.183$) nor sex ($F_{1, 11} = 0.89$; adjusted $p = 0.171$) were significant predictors of item interaction.

Lying Down

Lying down behaviour was not significantly predicted by location ($F_{5, 11} = 2.54$; adjusted $p = 0.169$) or sex ($F_{1, 11} = 0.44$; adjusted $p = 0.2$).

Social Interaction

Location ($F_{5, 11} = 3.92$; adjusted $p = 0.08$) nor sex ($F_{1, 11} = 0.45$; adjusted $p = 0.209$) were significant predictors of social interaction. The original p-value for social interaction was significant but after adjusting the p-values, social interaction for locations had a $p>0.05$.

Preening

Preening behaviour was not significantly predicted by location ($F_{5, 11} = 1.173$; adjusted $p = 0.253$) or by sex ($F_{1, 11} = 0.57$; adjusted $p = 0.328$).

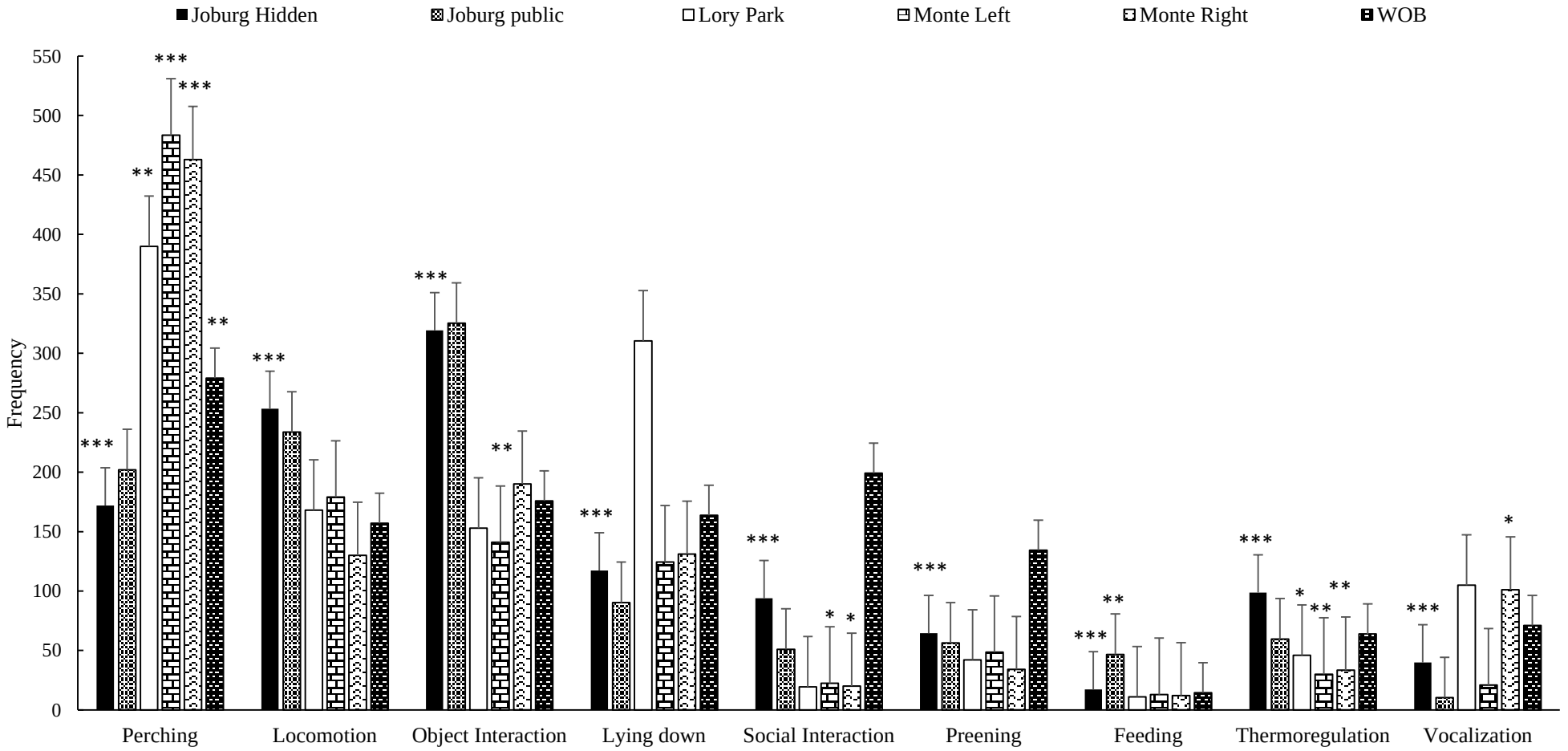


Figure 12: The frequency recorded for 9 categorises of behaviours in six captive ground hornbill populations over 12 hours, in the Gauteng and Western Cape provinces of South Africa. Bars denote the mean proportions calculated from each individual in each population and error bars are Standard Error. Asterisks indicate significant differences between populations for each behaviour.

Feeding

Location was a significant predictor of feeding behaviour ($F_{5, 11} = 8.57$; adjusted $p = 0.029$). Feeding by the Joburg public display ground hornbills was significantly greater than by ground hornbills at all the other 5 institutions ($p < 0.026$; Figure 12). The other institutions were similar and did not differ significantly in their feeding behaviour ($p>0.05$). Sex was not a significant predictor of feeding behaviour ($F_{1, 11} = 0.59$; adjusted $p = 0.235$).

Thermoregulation

Neither location ($F_{5, 11} = 3.51$; adjusted $p = 0.117$) nor sex ($F_{1, 11} = 3.14$; adjusted $p = 0.122$) were significant predictors of thermoregulation.

Vocalisation

Vocalisation was not significantly predicted by location ($F_{5, 11} = 4.78$; adjusted $p = 0.071$) or by sex ($F_{1, 11} = 1.87$; adjusted $p = 0.132$). The original p-value for vocalisation was significant but after adjusting the p-values, the location had a $p>0.05$.

The transactional (two-way social) interactions of captive ground hornbills

Socio-metric matrix analyses were used to establish the patterns of interactions of individuals in each location. These analyses were used to detect individual differences in the levels of amicable and aggressive behaviour displayed and received by each individual in the Joburg Zoo hidden display and the WOB population. I analysed only the amicable interactions between the individuals in the Johannesburg Zoo public display, Lory Park, as well as Monte Casino Bird Gardens due to the very few instances of aggressive interactions in these populations.

Johannesburg Zoo

Joburg public enclosure

Of the three individuals in Joburg public display group, levels of amicable interactions displayed did not differ from chance in any of the dyadic combinations (Table 3).

Table 3: Socio-metric matrix of the amicable interactions between the three individuals in the Joburg Public enclosure (z score; p-value). Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself.

	TINTO'12	NEBO'07	NTWANANA'95
TINTO'12	*	28; 0.625	28; -0.599
NEBO'07	29; -0.589	*	28; 0.612
NTWANANA'95	20; 0.698	11; -0.751	*

Joburg hidden enclosure

Levels of amicable (Table 4) and aggression interactions (Table 5) did not differ from chance in any of the dyadic combinations for the three individuals in the Joburg hidden population.

Table 4: Socio-metric matrix of the amicable interactions between the three individuals in the Joburg Hidden enclosure (z score; p-value). Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself.

	JASPER'13	RHINOROAD'11	JANOVSKY'12
JASPER'13	*	54; 0.534	34; -0.598
RHINOROAD'11	47; -0.541	*	38; 0.599
JANOVSKY'12	31; 0.635	27; -0.622	*

Table 5: Socio-metric matrix of the aggressive interactions between the three individuals in the Joburg Hidden enclosure (z score; p-value). Values indicate the aggressive behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no aggression directed by a bird to itself.

	JASPER'13	RHINOROAD'11	JANOVSKY'12
JASPER'13	*	16; -0.551	2; 0.139
RHINOROAD'11	18; 0.514	*	1;-0.123
JANOVSKY'12	3; -0.714	11; 0.699	*

Lory Park

The results showed that both individuals in the Lory Park enclosure showed that both birds displayed amicable behaviour greater than chance (Table 6).

Table 6: Socio-metric matrix of the amicable interactions between the two individuals at Lory Park (z score; p-value). Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself. Significant values are shown in bold.

	PRICILLA'06	ELVIS'92
PRICILLA'06	*	**19; 0.010**
ELVIS'92	**18; 0.010**	*

Monte Casino Bird Gardens

The results showed that the individual birds in both enclosures displayed amicable behaviour greater than chance (Table 7 and 8).

Table 7: Socio-metric matrix of the amicable interactions between the two individuals in the Monte Right enclosure (z score; p-value). Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself. Significant values are shown in bold.

	TSUWANE_1991	DEREK_1991
TSUWANE_1991	*	**13; 0.010**
DEREK_1991	**16; 0.010**	*

Table 8: Socio-metric matrix of the amicable interactions between the two individuals in the Monte Left enclosure (z score; p-value). Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row. The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself. Significant values are shown in bold.

	Hugo_1991	Priscilla_1991
Hugo_1991	*	**18; 0.010**
Priscilla_1991	**22; 0.010**	*

World of Birds

There were six individual ground hornbills in the WOB enclosure. Levels of amicable interactions in the dyads did not deviate significantly from chance (Table 9). Similarly, aggressive interactions in dyads mostly did not deviate significantly from chance (Table 10). However, one juvenile (T134) directed significant levels of aggression to another juvenile (T129) (Table10). All six members of the WOB enclosure showed equal amicability across the population, whereas there was only a significant aggression display between T84 (Adult Male) and T85 (Female) (Table 10).

Table 9: Socio-metric matrix of the amicable interactions between the six individuals at the Hout Bay World of Birds. Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row (z score; p-value). The diagonal of asterisks indicate no amicable behaviour directed by a bird to itself.

	T85 (Female)	T129 (Juvenile)	T147 (Juvenile)	T134 (Juvenile)	KHUMI_2013 (Male)	T84(Male)
T85 (Female)	*	4; -0.911	1; -0.945	1; -0.592	1; -0.368	407; 0.130
T129 (Juvenile)	0; -0.102	*	87; 0.782	30; 0.129	9; 0.530	2; -0.957
T147 (Juvenile)	0; -0.925	85; 0.277	*	16; 0.679	6; 0.358	0; -0.905
T134 (Juvenile)	0; -0.631	25; 0.106	21; 0.885	*	8; 0.834	0; -0.614
KHUMI_2013	0; -0.395	7; 0.426	9; 0.603	6; 0.644	*	0; -0.384
T84 (Male)	412; 0.135	0; -0.980	0; -0.959	0. -0.617	0; -0.407	*

Table 10: Socio-metric matrix of the aggressive interactions between the six individuals at the Hout Bay World of Birds. Values indicate the amicable behaviour displayed individuals in listed in the first column to individuals listed in the first row (z score; p-value). The diagonal of asterisks indicate no aggression directed by a bird to itself. Significant values are shown in bold.

	T85 (Female)	T129 (Juvenile)	T147 (Juvenile)	T134 (Juvenile)	KHUMI_2013 (Male)	T84 (Male)
T85 (Female)	*	0; -0.170	0; -0.115	0; -0.688	0; -0.329	3; 0.773
T129 (Juvenile)	0; -0.988	*	7; 0.567	3; 0.269	1; 0.534	0; -0.123
T147 (Juvenile)	0; -0.104	12; 0.771	*	4; 0.886	0; -0.190	0; -0.131
T134 (Juvenile)	0; -0.706	**6; 0.021**	4; 0.237	*	1; 0.109	0; -0.889
KHUMI_2013 (Male)	0; -0.328	2; 0.622	1; 0.136	0; -0.688	*	0; -0.411
T84 (Male)	2; 0.480	2; -0.434	1; -0.529	0; -0.911	0; -0.422	*

Johannesburg Zoo Hidden Enclosure

The middle right (MR) zone was used the most by all three ground hornbill individuals (Table 11). This zone contained the entrance gate and the feeding station. The second most used zone was the back right zone which contained the boundary fence closest to the foot traffic of people and had constant shade from the large tree. The two least used zones were the upper front left zone and the upper back left zone which both consisted of large perching poles.

Table 11: The frequency of occurrence by three ground hornbills in 12 zones in the Joburg hidden enclosure shown in descending order with the main physical contents in each zone

Zone from most used to least used	**Frequency of occurrence**	**Zone contents**
Middle Right	474	The entrance gate and feeding station
Back Right	362	The boundary fence closest to the foot path, shade from the large tree
Front Left	329	The boundary fence closest to the foot path
Front Right	313	The boundary fence closest to the foot path
Upper Middle Left	240	The nest box
Middle Left	105	A empty rock pool
Upper Back Right	86	Large perching pole
Upper Front Right	63	Large perching pole
Back Left	55	Shade from the tree
Upper Front Left	38	Larger perching pole
Upper Back Left	20	Large perching pole
Upper Middle Right	18	Large perching pole

Overall, the space use of ground hornbills at the Joburg Hidden enclosure was significantly influenced by the zone (χ^2_{11} = 1625.58; p <0.001) and the combination of individual*zone (χ^2_{22} = 290.29; p < 0.001). However, individual on its own had no significant influence on space use (χ^2_2 = 3.12 p = 0.210). Of the 12 zones within the Joburg hidden enclosure, occurrences in all zones differed significantly from the Back Left (BL) zone used as the reference category, except for two zones (Upper Front Left and Upper Front Right zones; Table 12).

Table 12: Statistical output comparing the use of 11 zones compared to the Back Left zone (used as the reference category) in the Joburg Hidden enclosure and their corresponding z and p values. Significant values are shown in bold.

Zone	**z value**	***P* value**
Back Right	13.02	**<0.001**
Front Left	12.28	**<0.001**
Front Right	11.89	**<0.001**
Middle Left	3.89	**0.001**
Middle Right	15.12	**<0.001**
Upper Back Left	-3.87	**0.0001**
Upper Back Right	2.59	**0.009**
Upper Front Left	-1.75	0.079
Upper Front Right	0.74	0.461
Upper Middle Left	9.86	**<0.001**
Upper middle Right	-4.11	**<0.001**

Individual Differences

In the Joburg Hidden enclosure, the three ground hornbills all used the Upper Middle Right section of the cage the most (Figure 13). Two of the individuals (Jasper_2013 and Janovsky_2012), used the upper middle right zone the least, whereas Rhino_Road_2011 used the upper front left and upper front right sections the least (Figure 13).

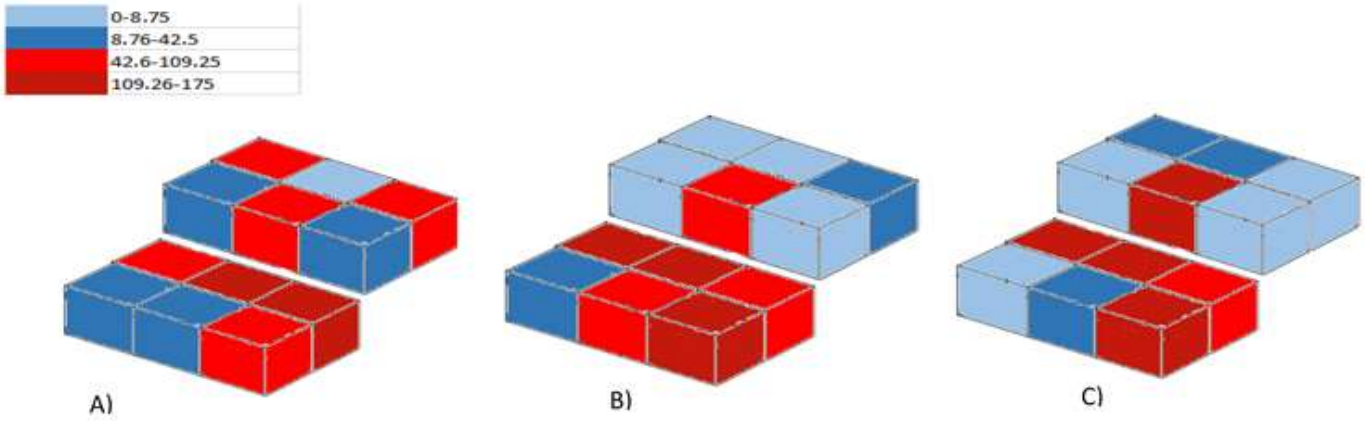


Figure 13: A diagrammatic representation of the space use by three ground hornbills, A) Jasper_2013, B) Janovsky_2012 and C) Rhino_Road_2011, in 12 zones of the Joburg Zoo hidden display enclosure. The colours indicate interquartiles of the frequency of zone use. Colour codes are provided as four concentrations based on frequency of occurrence of each individual per zone. The quartiles of the scores were used to assign the colour codes. The dark red (maroon) colour represented a zone that had a high number of visits (calculated in the fourth quartile), followed by the lighter red (third quartile), the dark blue colour (second quartile) and lastly the light blue colour (first quartile).

Sex differences

Comparing the space use of the male and female individuals showed that the frequency of entry was fairly similar, although the males used the Front Left and Upper Middle Left zones more often than the female (Figure 13).

Johannesburg Zoo Public Display

The results showed that the ground hornbills mostly used the Back Left zone (Table 14). This zone contained a large perching platform and shade from a large tree. The second most used zone was the upper front left zone which contained a nest box and a small river stream (Table 14). The two least used zones were the upper middle right zones and the upper front right zones which both consisted of a tree stump and a medium sized tree.

Table 13: The frequency of occurrence of the three ground hornbills in 12 zones in the Joburg public enclosure shown in descending order with the main physical contents in each zone.

Zone from most used to least used	**Frequency of entry**	**Zone contents**
Back Left	566	Large perching platform and shade from a large tree
Upper Front Left	450	The nest box and a small riverine
Front Left	321	The boundary fence available for public interaction, entrance gate and food station
Middle Right	293	Boundary fence next to saddle bill storks and small riverine
Back Right	178	Shade from tree
Upper Back Left	159	Perch and shade from a large tree
Front Right	110	The boundary fence available for public interaction and entrance gate
Upper Middle Right	55	The large perching pole and a small riverine
Middle Left	16	Boundary fence next to blue cranes and small riverine
Upper Back Right	8	Large Tree and nest box
Upper Middle Left	2	A tree stump
Upper Front Right	2	A medium sized tree

The space use of ground hornbills at the Joburg public enclosure was significantly influenced by the zone (χ^2_{11} = 2332.96; p<0.001*)* and the interaction between individual*zone (χ^2_{22} = 482.78; p<0.001). However, ID had no significant influence on space use (χ^2_2 = 0.00; p= 1.000) (Table 15). The Back Left Zone was the reference zone. Of the 12 zones within the Joburg public enclosure, the occurrence of ground hornbills in all zones differed significantly from the Back Left (BL) zone used as the reference category, except for two zones (Upper back right and the Upper Front Right zone; Table 15).

Table 14: Statistical output comparing the use of 11 zones compared to the Back Left zone (used as the reference category) in the Joburg Public enclosure and their corresponding z and p values. Significant values are shown in bold.

Zone	**z value**	***P* value**
Back Right	-8.378	**<0.001**
Front Left	-7.120	**<0.001**
Front Right	-8.378	**<0.001**
Middle Left	-6.414	**<0.001**
Middle Right	-3.929	**<0.001**
Upper Back Left	-3.564	**0.001**
Upper Back Right	0.000	0.999
Upper Front Left	-7.120	**<0.001**
Upper Front Right	0.000	0.999
Upper Middle Left	-6.414	**<0.001**
Upper middle Right	-9.314	**<0.001**

Individual Differences

When comparing the three individuals in the Joburg public enclosure, Tinto'12 used the back left zone the most, and used the upper back right and upper middle right the least. Nebo'07 used the middle left zone the most, and the upper front left the least. In contrast, Rhino_Road_2011 used the upper middle left sections the most and the Front Left, Upper Back Right, Upper Front Left and the Upper Middle Right the least (Figure 14).

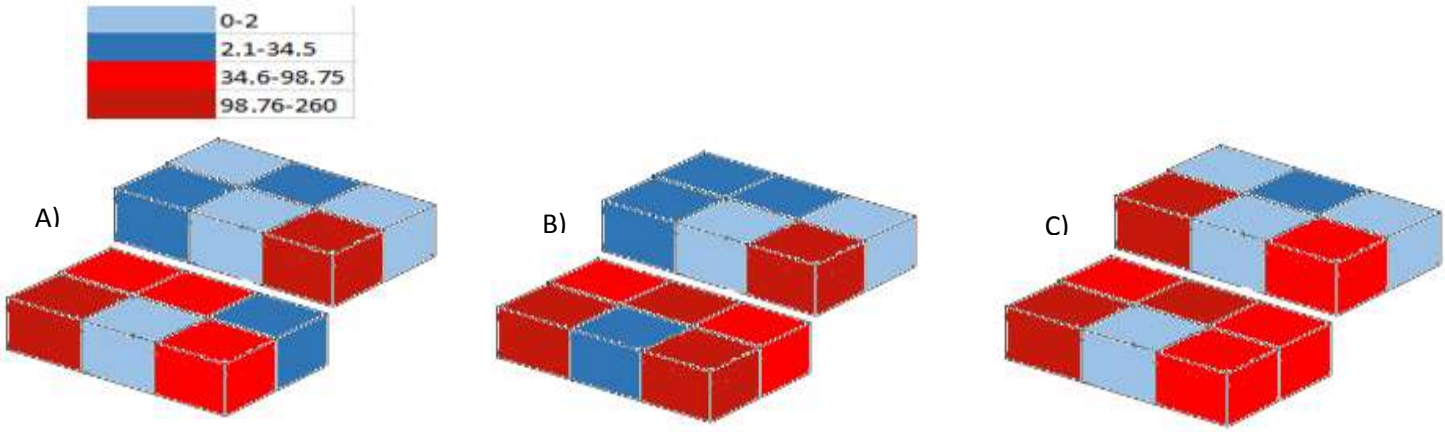


Figure 14: A diagrammatic representation of the space use by three ground hornbills, A) Tinto'12, B) Nebo'07and C) Ntwanana'95, in 12 zones of the Joburg Zoo public display enclosure. The colours indicate interquartiles of the frequency of zone use (see Figure 14)

Sex differences

The space use of the male and female individuals at the Joburg Public display showed no differences between the sexes except for females using the Upper Back Left zone more often than the males (Figure 14).

Monte Casino Bird Gardens Right Enclosure

Overall, the most used zone by the two birds in the enclosure was the Upper Front Right zone (Table 17). This zone contained a large perching pole. The second most used zone was the front left zone which contained a small brick wall and the boundary fence where they were normally fed crickets and meal worms (Table 17). The two least used zones were the upper middle right zones and the upper middle left zones which both consisted of a tree stump.

Table 15: The frequency of occurrence of two ground hornbills in 12 zones in the Monte Right enclosure shown in descending order with the main physical contents in each zone

Zone from most used to least used	**Frequency of entry**	**Zone contents**
Upper Front Right	875	A large perching pole
Front Left	648	A small brick wall and the boundary fence where they normally get fed crickets and meal worms
Upper Back Right	323	A large perching pole and nest box
Back Left	120	The feeding station and water source
Upper Front Left	98	A large perching pole
Front Right	48	A small brick wall and the boundary fence where they normally get fed crickets and meal worms
Middle Left	32	The boundary fence that is closest to the other ground hornbill pair
Back Right	6	Nothing
Middle Right	6	The outside boundary fence
Upper Back Left	3	A large perching pole
Upper Middle Right	3	A tree stump
Upper Middle Left	0	Nothing

The space use by ground hornbills at the Monte right enclosure was significantly influenced by the zone (χ^2_{11} = 2811.02; p<0.001) and the influence of individual*zone (χ^2_{11} = 72.38 p<0.001). However, individual had no significant influence on space use (χ^2_1 = 0.00; p= 1.000). Of the 12 zones within the Monte right enclosure, the occurrence of ground hornbills in all zones differed significantly from the Back Left (BL) zone used as the reference category, except for three zones (Upper Back Left, Upper Middle Left and Upper Middle Right zones; Table 18).

Table 16: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Monte right enclosure and their corresponding z and p values. Significant values are shown in bold.

Zone	**z value**	***P* value**
Back Right	-4.059	**<0.001**
Front Left	8.083	**<0.001**
Front Right	-3.756	**0.001**
Middle Left	-3.338	**0.001**
Middle Right	-4.059	**<0.001**
Upper Back Left	0.000	0.999
Upper Back Right	6.428	**<0.001**
Upper Front Left	-2.181	**0.029**
Upper Front Right	12.925	**<0.001**
Upper Middle Left	0.000	0.999
Upper Middle Right	0.000	0.999

Individual Differences

When comparing the ground hornbill individuals in the Monte right enclosure, Priscilla'91 used the Upper Middle Left zone the most, and used the upper front left and upper back left the least. In contrast, Hugo'91 used the upper middle back right section the most, and Front Right, Middle Left, Upper Back Left, Upper Front Left the least (Figure 15).

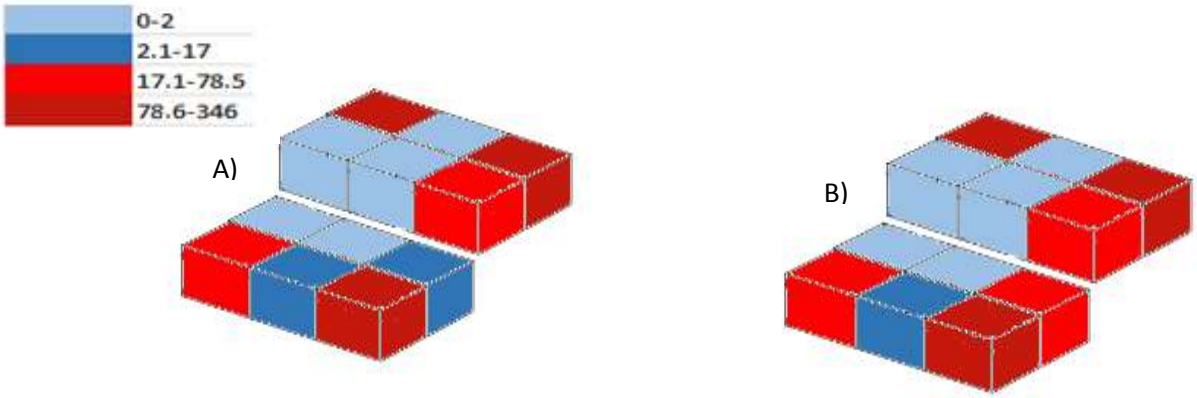


Figure15: A diagrammatic representation of the space use by two ground hornbills, A) Priscilla'91 and B) Hugo'91, in 12 zones of the Monte right enclosure display enclosure. The colours indicate interquartiles of the frequency of zone use (see Figure 14).

Sex differences

The male and female in the Monte Right display showed a similar frequency of entry into the same zones. However, the female used the Upper Back Right zone more often and the male used the Upper Back Right more often (Figure 15).

Monte Casino Bird Gardens Left Enclosure

Overall, the zone used the most by the ground hornbills was the Front Left zone and the Front Right zone (Table 20). Both zones contained a small brick wall and the boundary fence where they were normally fed crickets and meal worms. The two least used zones were the upper middle right zones and the upper Front left zones which both consisted of nothing.

Table 17: The frequency of occurrence by two ground hornbills in 12 zones in the Monte Left enclosure shown in descending order with the main physical contents in each zone.

Zone from most used to least used	**Frequency of entry**	**Zone contents**
Front Left	593	A small brick wall and the boundary fence where they normally get fed crickets and meal worms
Front Right	589	A small brick wall and the boundary fence where they normally get fed crickets and meal worms
Upper Back Right	449	A large perching pole and nest box
Upper Front Right	263	A large perching pole
Back Left	105	Food station and water source
Upper Back Left	823	A large perching pole
Middle Left	27	The boundary fence
Middle Right	27	The boundary fence that is closest to the other ground hornbill pair
Back Right	26	The entrance gate
Upper Middle Left	0	Nothing
Upper Middle Right	0	Nothing
Upper Front Left	0	Nothing

The space use by ground hornbills at the Monte Casino Bird Gardens left enclosure was significantly influenced by the zone (χ^2_{11} = 2187.33; p<0.001) and individual*zone (χ^2_{11} = 165.92; p <0.001). However, individuals had no significant influence on space use (χ^2_1 = 0.00; p= 1.000). Of the 12 zones within the Monte Casino left enclosure, the occurrence of ground hornbills in all zones differed significantly from the Back Left (BL) zone used as the reference category, except for three zones (Upper Back Right, Upper Middle Right and Upper Front Right zones; Table 21).

Table 18: Statistical output comparing the use of 11 zones compared to the Back Left zone was used as the reference category in the Monte Left enclosure and their corresponding z and p values. Significant values are shown in bold.

Zone	**z value**	***P* value**
Back Right	21.03	**<0.001**
Front Left	-3.77	**0.001**
Front Right	9.67	**<0.001**
Middle Left	6.11	**<0.001**
Middle Right	-2.89	**0.004**
Upper Back Left	-3.94	**<0.001**
Upper Back Right	-0.88	0.378
Upper Front Left	8.66	**<0.001**
Upper Front Right	0	0.999
Upper Middle Left	7.34	**<0.001**
Upper Middle Right	0	0.999

Individual Differences

When comparing the individuals in the Monte left enclosure, Tsuwane'91 used the Back Right zone and Upper Middle Left zone the most, and used the front right zone the least. In contrast, Derek'91 used the middle right section the most, and Front Left and Upper Middle Right the least (Figure 16).

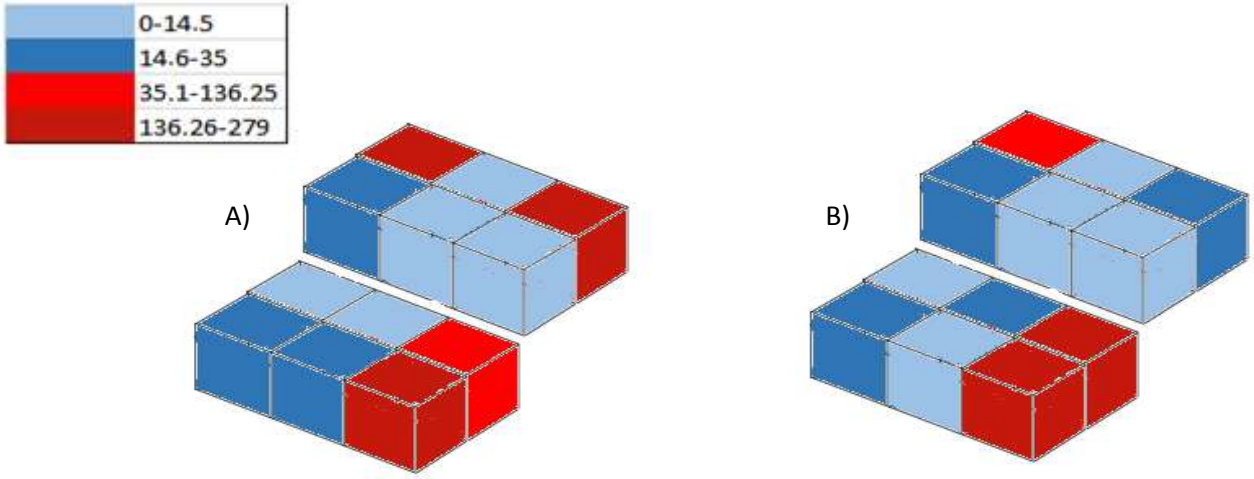


Figure 16: A diagrammatic representation of the space use by two ground hornbills, A) Tsuwane'91, B) Derek'91, in 12 zones of the Monte left enclosure display enclosure. The colours indicate interquartiles of the frequency of zone use (see Figure 14).

Sex differences

The space use of the male and female at the Monte Left display was similar for the most part, with just males using the Front Right zone much more than the female (Figure 16).

Lory Park

The space use at the Lory Park enclosure was significantly influenced by the zone (χ^2_{11} = 2700.54; p< 0.001) and the interaction between individual*zone (χ^2_{11} = 263.59; p< 0.001). However, ID had no significant influence on space use (χ^2_1 = 0.00; p=1.000). Of the 12 zones within the Lory Park enclosure, the occurrence of ground hornbills in five zones differed significantly from the Back Left (BL) zone which used as the reference category, and six zones did not differ significantly from the reference category (Table 23).

Table 19: The 12 zones in the Lory Park enclosure and their corresponding z and p values

Zone	**z value**	**P value**
Back Right	-1.35	0.178
Front Left	7.09	**<0.001**
Front Right	7.36	**<0.001**
Middle Left	0	0.999
Middle Right	1.74	0.082
Upper Back Left	8.59	**<0.001**
Upper Back Right	8.19	**<0.001**
Upper Front Left	5.06	**<0.001**
Upper Front Right	0	0.999
Upper Middle Left	0	0.999
Upper Middle Right	0.27	0.781

The zone most used by the two ground hornbills was the Upper Back Left zone (Table 24). This zone contained a large perching platform and the left boundary fence that is closest to the Northern ground hornbill pair. The second most used zone was the front right zone which contained the front boundary fence available for public interaction (Table 24). The two least used zones were the upper middle left zones and the upper front right zones which both consisted of nothing.

Table 20: The frequency of occurrence by two ground hornbills in 12 zones in the Lory Park enclosure shown in descending order with the main physical contents in each zone.

Zone from most used to least used	**Frequency of entry**	**Zone contents**
Upper Back Left	593	Large perching platform with the boundary fence that is closest to the Northern ground hornbill pair
Front Right	348	The boundary fence available for public interaction
Upper Back Right	222	Large perching platform with the boundary fence that is closest to the fish eagle pair
Front Left	165	The boundary fence available for public interaction
Upper Front Left	55	Large perching pole and boundary fence that is available for public interaction
Back Left	22	Nest box and feeding station and shade from the large perching platform above
Middle Right	20	The small river
Upper Middle Right	10	Large perching pole
Back Right	5	Feeding station and shade from the large perching platform above
Middle Left	0	Nothing
Upper Middle Left	0	Nothing
Upper Front Right	0	Nothing

Individual Differences

When comparing the individuals in the Lory Park enclosure, Pricilla'06 used the Upper Front Left zone the most, and used the Front Left and Upper Middle Right zone the least. Elvis'92 used the middle right section the most, and Upper Back Left zone the least (Figure 17).

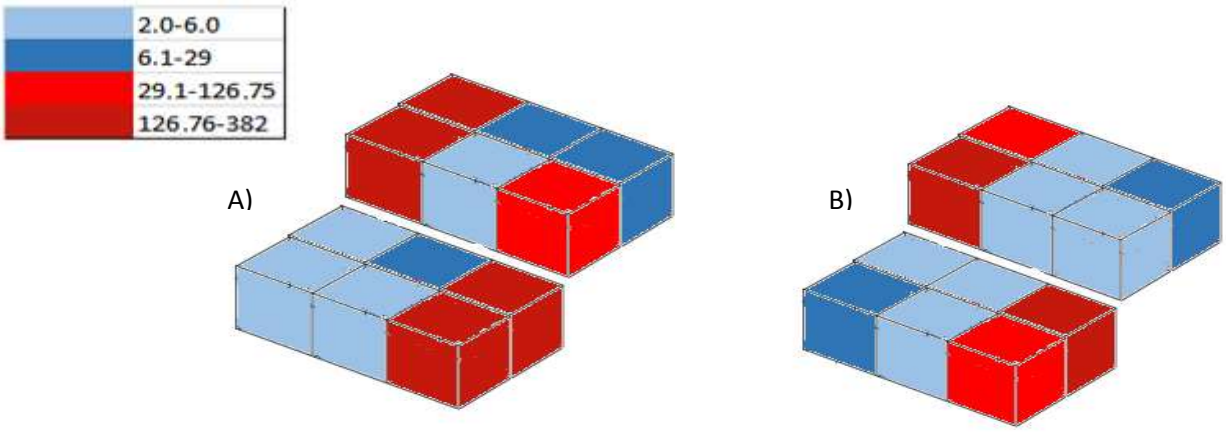


Figure 17: A diagrammatic representation of the space use by two ground hornbills, A) Pricilla'06 and B) Elvis'92, in 12 zones of the Lory park enclosure display enclosure. The colours indicate interquartiles of the frequency of zone use (see Figure 14).

Sex differences

The space use of the male and female at Lory Park showed large differences. The female used the Back Right, Upper Back Left and Upper Middle Left zones much more often than the male, whereas the male tended to use the Front Left and Front Right more than the female (Figure 17).

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle

Startle Tests

From the video footage, the ground hornbills performed one or more of the 9 behaviours initially before the startle noise was emitted. The time taken to resume regular behaviour after being exposed to a startle sound (i.e. a siren) was not significantly influenced by location (χ_5^2 = 5.73, p= 0.330; Figure 18a), sex (χ_1^2 = 0.57, p= 0.681; Figure 19) or by replicate number (χ_2^2 = 2.26, p= 0.442; Figure 20). Figure 18a shows similar responses by ground hornbills to resume activity following the sound startle test in the 6 populations, although the duration of time for individuals to resume normal activity was longest in Lory Park, followed by WOB, Joburg Hidden enclosure and Monte Left enclosure (Figure 18).

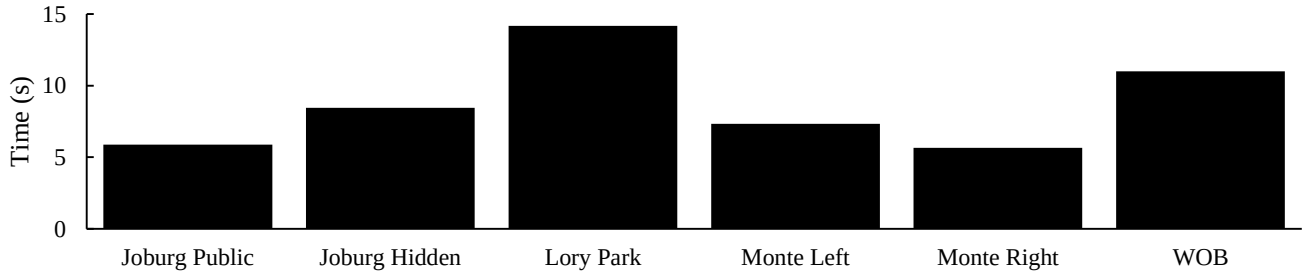


Figure 18: The comparison of the latency (total duration) to resume normal activity by ground hornbills in 6 enclosures.

The latency to resume activity following a startle was similar in the sexes (Figure 19).

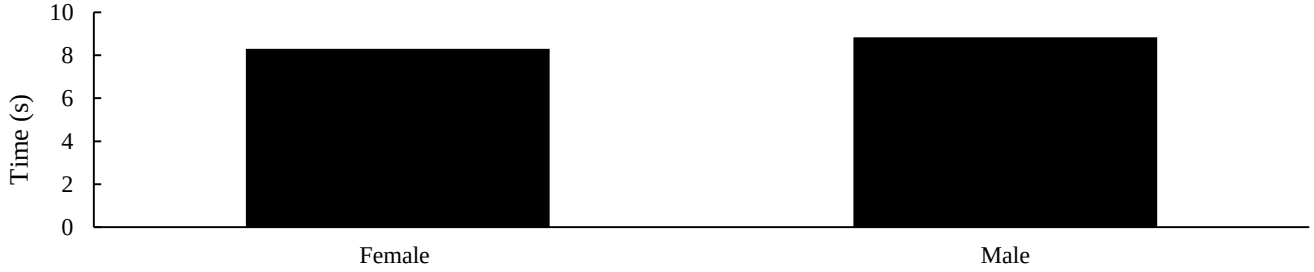


Figure 19: The latency (total duration) to resume normal activity between the two sexes in all institutions.

Replicates

Startle tests were conducted in three replicates per session per ground hornbill enclosure. The latency to resume normal activity in the three trial replicates was similar with a slightly greater response in replicate 2 (Figure 20).

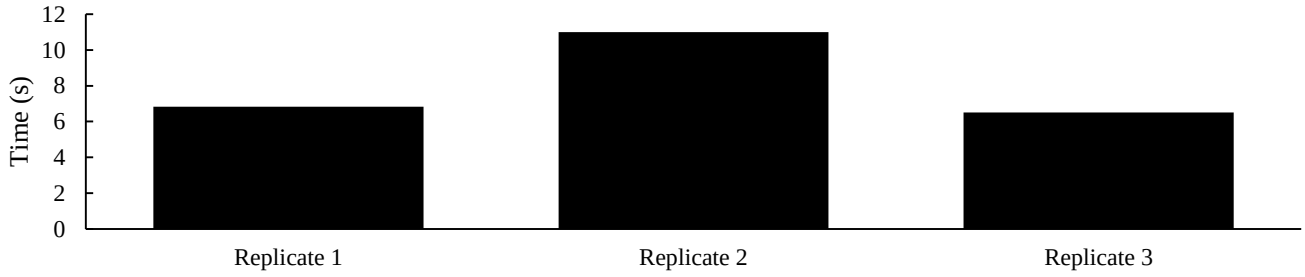


Figure 20: The latency (total duration) to resume normal activity by ground hornbills in three replicates

Individual Differences

I compared the startle response of individual ground hornbills within the Joburg Zoo Hidden Enclosure, and found no significant difference in startle behaviour amoung the three individuals (χ_4^2 = 1.99, p= 0.736; Figure 21). Similarly, individuals did not differ in their response to a startle in the Joburg Public Enclosure (χ_4^2 = 2.21, p= 0.697; Figure 22).

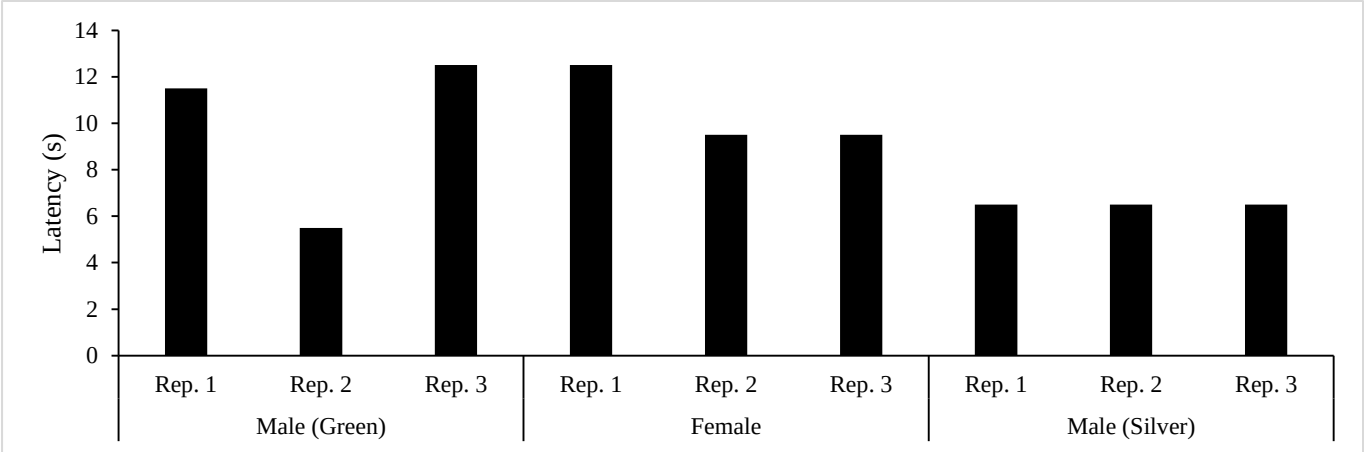


Figure 21: The latency (total duration) to resume normal activity by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates (Rep).

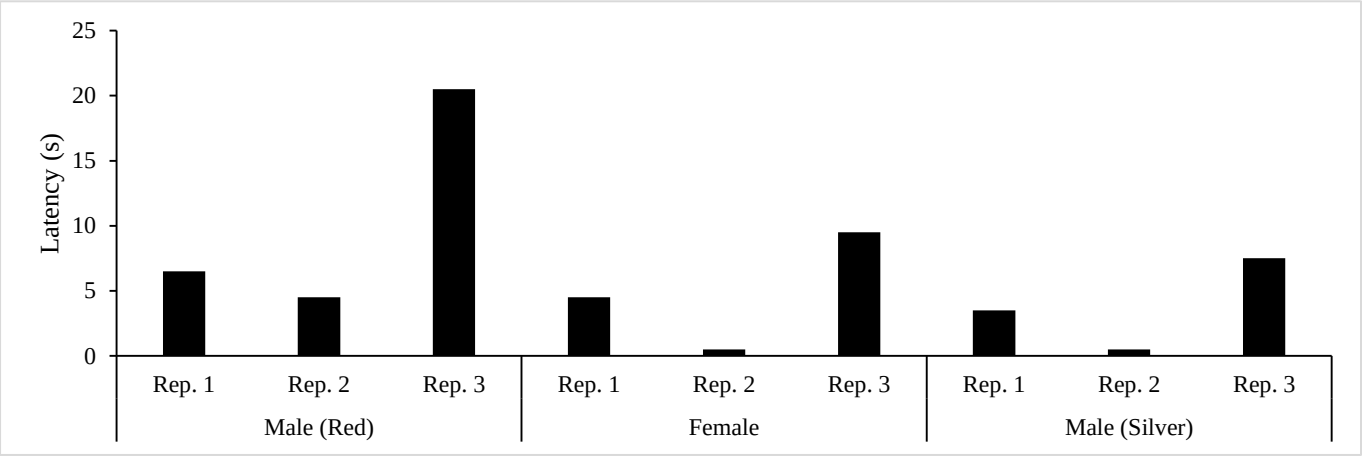


Figure 22: The latency (total duration) to resume normal activity by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates (Rep)

In the Monte Casino Right Enclosure, the two ground hornbills differed significantly in their responses to a startle (χ_2^2 = 9.99, p= 0.007; Figure 23). The female took less time to resume normal activity in replicate 2 and the male resumed activity quicker in replicate 3 (contribution to chi-squared analysis; Figure 23). Similarly, there was a significant difference in the startle response between individuals at the Monte Casino Bird Gardens Left Enclosure (χ_2^2 = 28.09, p < 0.001; Figure 24). The female took the longest to resume activity after the startle in replicate 1 and the male took the shorter time to resume activity in replicate 3 (contribution to chi-squared analysis; Figure 24).

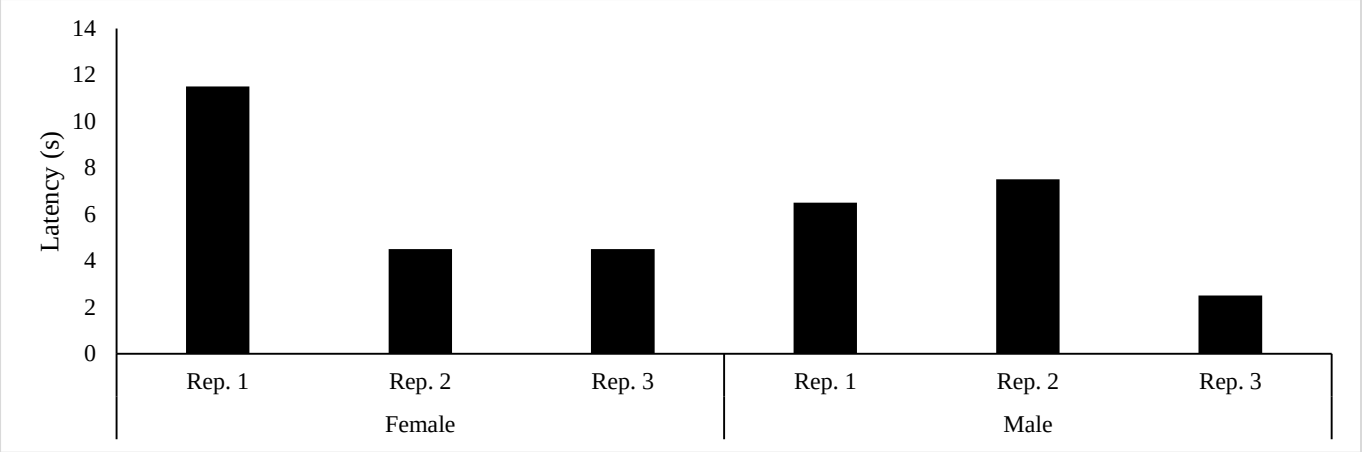


Figure 23: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Monte Casino Bird Gardens Right Enclosure in three replicates (Rep).

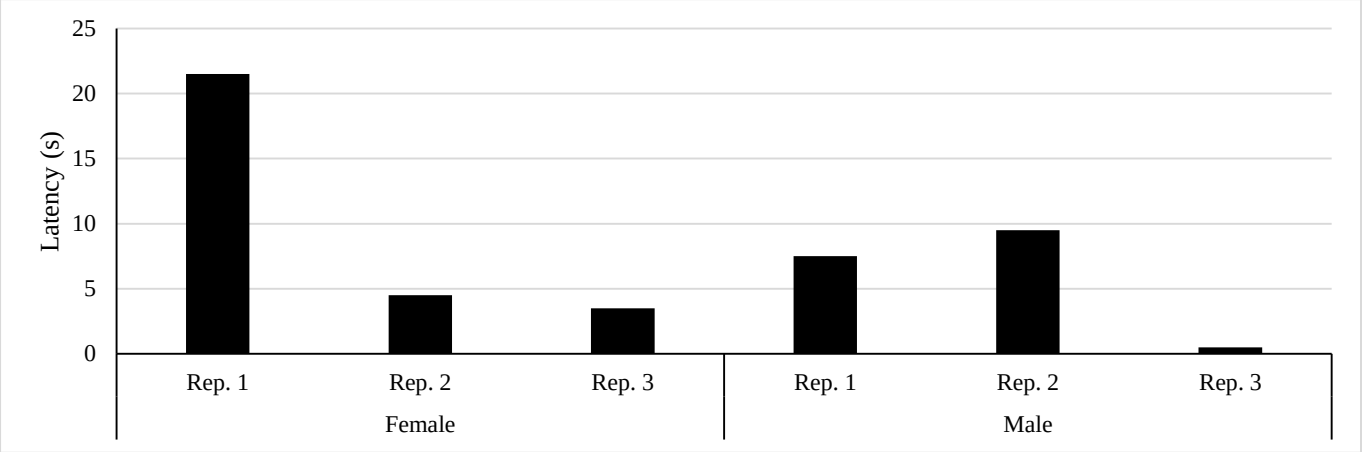


Figure 24: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Monte Casino Bird Gardens Left Enclosure in three replicates (Rep).

In the Lory Park Enclosure, the two individuals differed significantly in their response to a startle (χ_2^2 = 32.93, p< 0.001; Figure 25). The female took a shorter time to resume activity in replicate 2 compared to the male and took longer to respond to a startle in replicate 3 (contribution to chi-squared analysis; Figure 25).

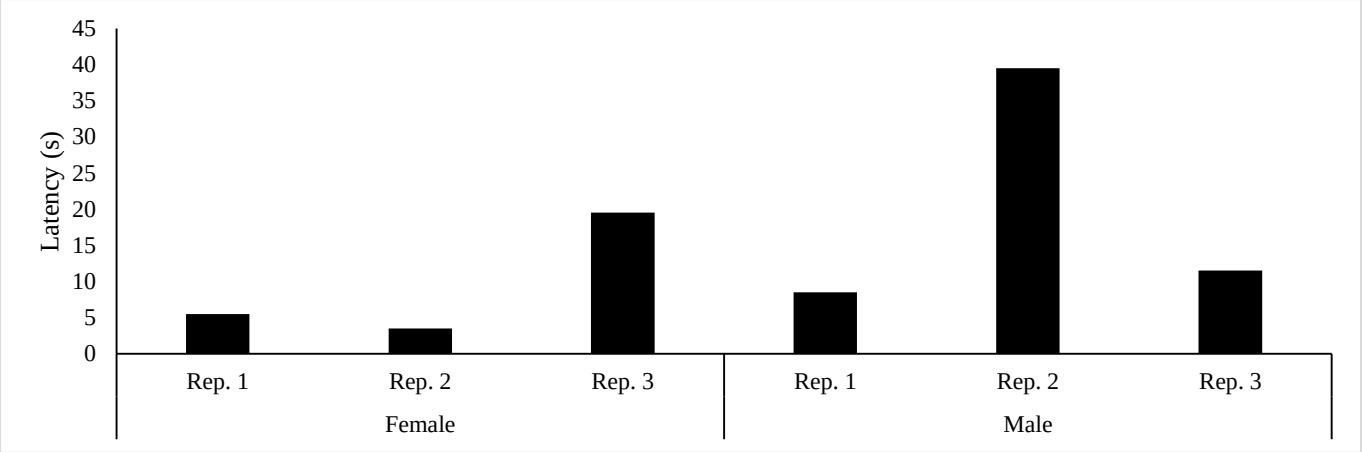


Figure 25: The latency (total duration) to resume normal activity by the two individual ground hornbills at the Lory Park Enclosure in three replicates (Rep).

In the World of Birds Enclosure, the six individuals differed significantly in their response to the startle (χ^2_{10} = 133, 29, p< 0.001; Figure 26). The male, WOB_2 was quickest to resume activity after the startle. In contrast, WOB_3 (male) and WOB_5 (juvenile) showed the slowest latency to resume activity in replicates 1 and 2, and so too WOB_6 (juvenile) in replicate 2 (contribution to chi-squared analysis; Figure 26)

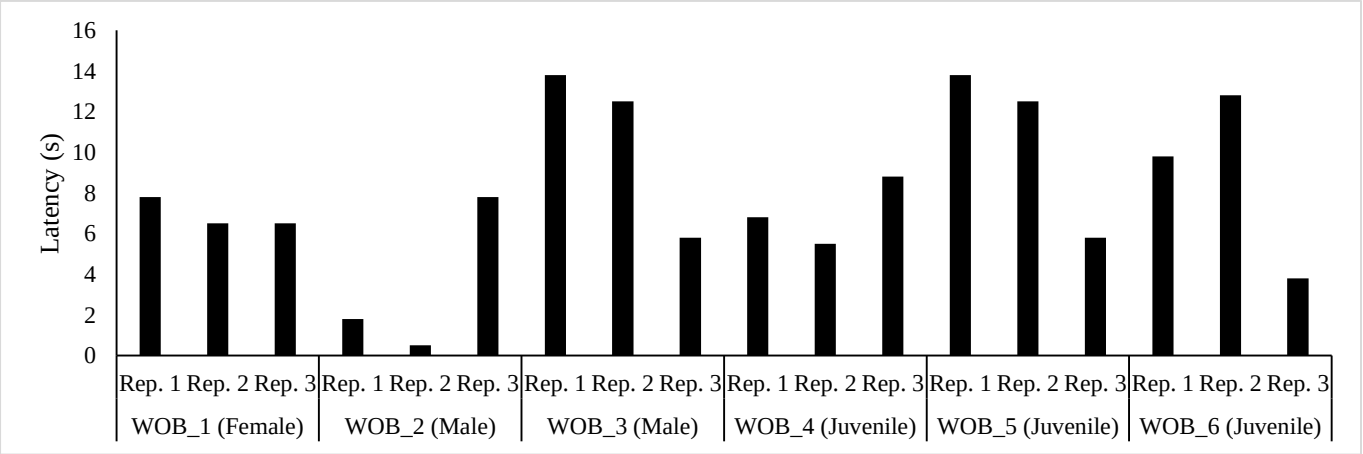


Figure 26: The latency (total duration) to resume normal activity by the six individual ground hornbills at the World of Birds Enclosure in three replicates (Rep).

Novel Object Tests

Approach

Location

The latency to touch a novel object was significantly influenced by location (χ_5^2 = 1279.52, p < 0.001; Figure 27). The Tukey post-hoc tests (*lsmeans* test) showed that the WOB birds took significantly longer to approach the novel object (p < 0.001).

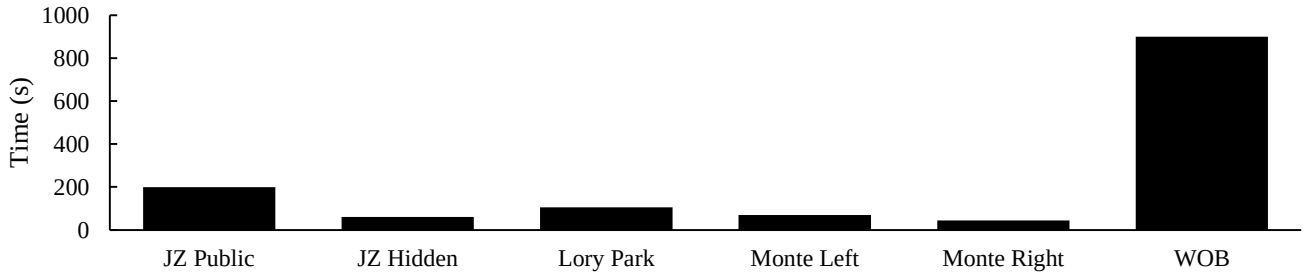


Figure 27: The latency (total duration) to approach the novel object by ground hornbills in in the 6 enclosures.

Sex

The time taken to approach and touch the novel object was not significantly influenced by sex (χ_1^2 = 1.45, p= 0.221; Figure 28).



Figure 28: The latency (total duration) to approach the novel object by the two ground hornbill sexes

Replicates

The latency to touch a novel object was significantly influenced by replicate number (χ_2^2 = 18.30, p < 0.001; Figure 19c). The *lsmeans* r showed latency was greater in replicate 1 compared to replicate 3 (t_6= 3.23; p= 0.041; Figure 29).

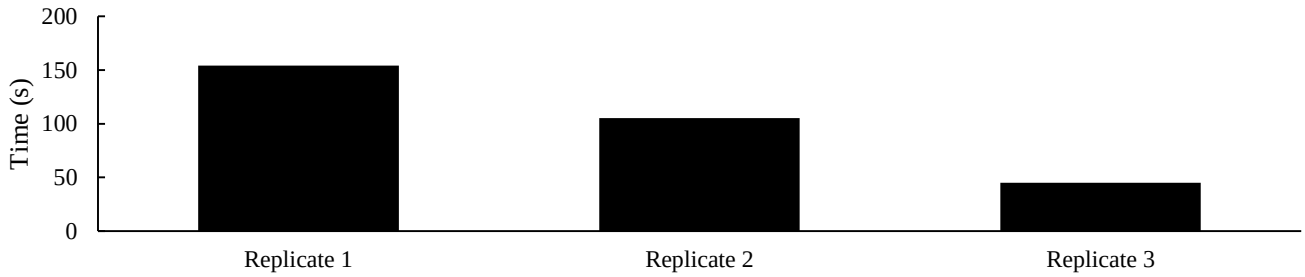


Figure 29: The latency (total duration) to approach the novel object by ground hornbills in the three replicates.

Individual Differences

There was a significant difference in the latency to approach the novel object in the three individuals in the Joburg Zoo Hidden Enclosure (χ_4^2 = 19, 98, p< 0.001; Figure 30). The one male (Green) showed the lowest latency in replicates 2 and 3. The other male (Silver) had the longest latency in replicate 1 (contribution to chi-squared analysis; Figure 30).

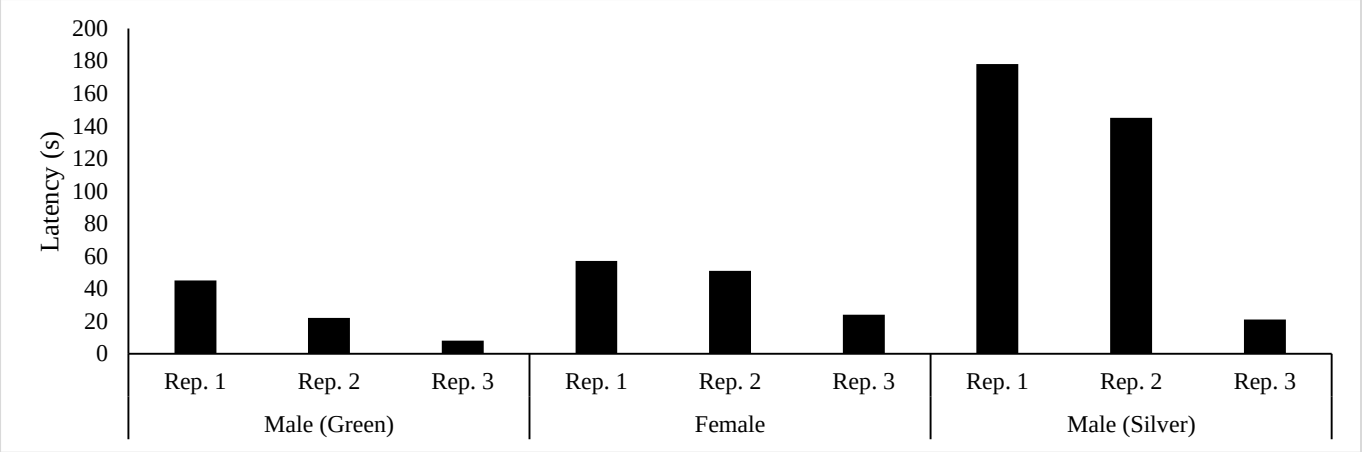


Figure 30: The latency (total duration) to approach the novel object by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates (Rep).

In the Joburg Zoo Public Enclosure, the three individuals differed in the latency to approach the novel object (χ_4^2 = 14.32, p= 0.006; Figure 31). The one male (Silver) showed the longest latency in replicates 1 and 3 (contribution to chi-squared analysis; Figure 31).

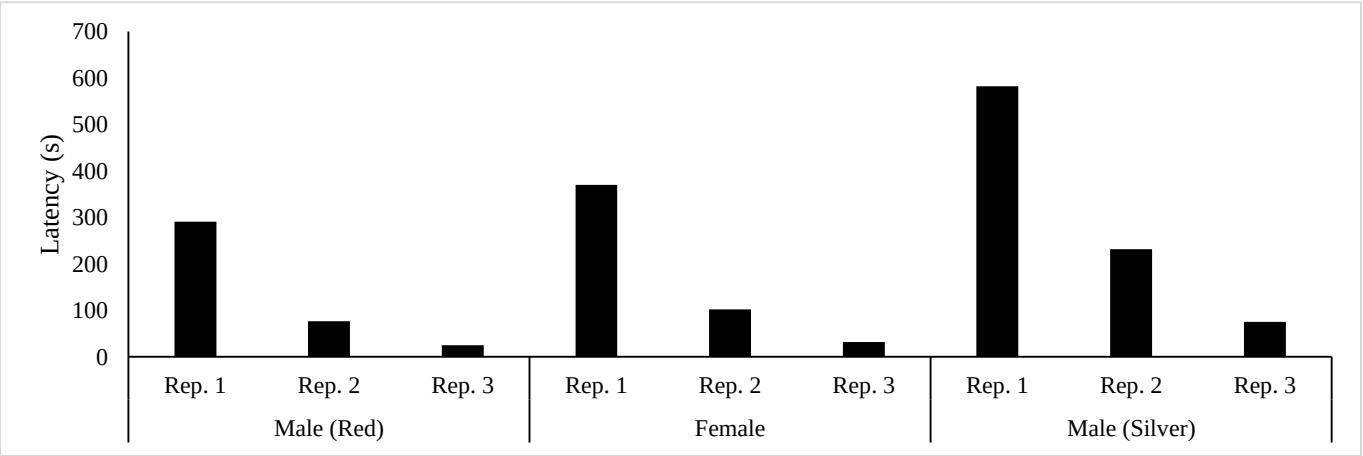


Figure 31: The latency (total duration) to approach the novel object by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates (Rep).

There was also a significant difference in the latency to approach the novel object by the two individuals in Monte Casino Bird Gardens Right Enclosure (χ_2^2 = 15.51, p< 0.001; Figure 32). The female consistently showed a greater latency to approach the novel object than the male, particularly in replicate 1 (contribution to chi-squared analysis; Figure 32). A significant difference in the latency was also recorded in the Monte Casino Bird Gardens Left Enclosure (χ_2^2 = 20.67., p < 0.001; Figure 33). The male took the longest to resume activity after the startle in replicate 2 compared to other individuals (contribution to chi-squared analysis; Figure 33).

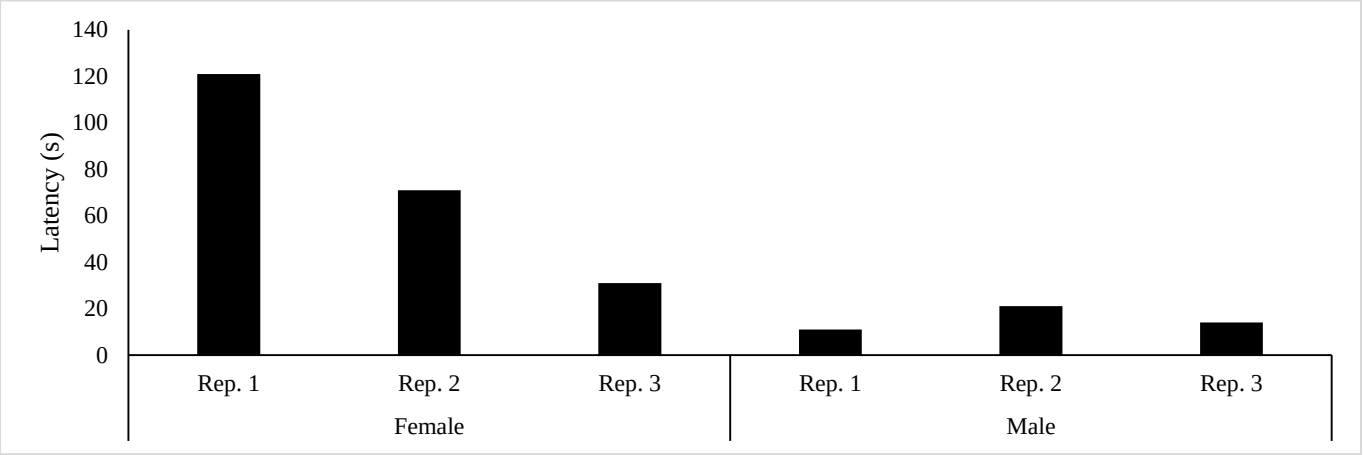


Figure 32: The latency (total duration) to approach the novel object by two three individual ground hornbills at the Monte Casino Bird Gardens Right Enclosure in three replicates (Rep).

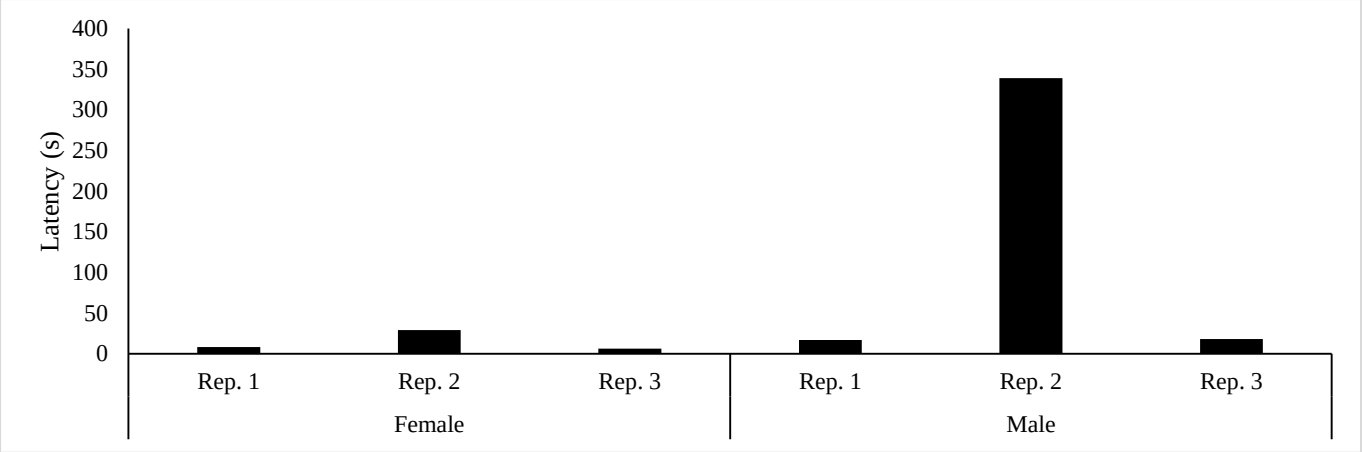


Figure 33: The latency (total duration) to approach the novel object by the two individual ground hornbills at the Monte Casino Bird Gardens Left Enclosure in three replicates (Rep).

At Lory Park, the two individuals differed significantly in their responses to the novel object (χ^2_2 = 13.04, p= 0.001; Figure 34). The male consistently took longer to approach the novel object than the female, with the longest latency in replicate 3 (contribution to chi-squared analysis; Figure 34).

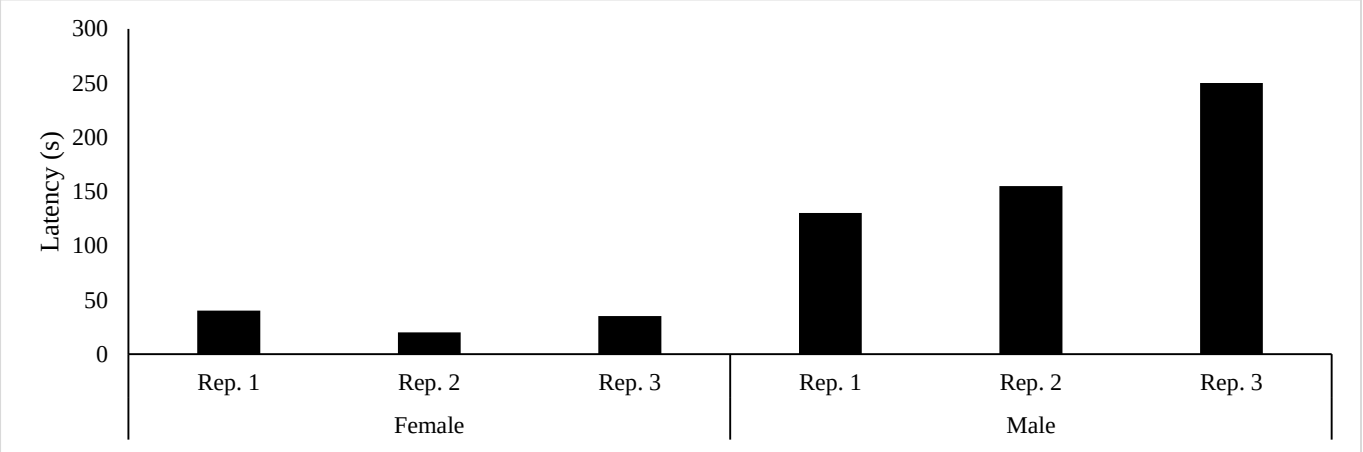


Figure 34: The latency (total duration) to approach the novel object by the two individual ground hornbills at the Lory Park Enclosure in three replicates (Rep).

In the World of Birds, none of the six individuals interacted with the novel object, so no analyses were conducted.

Interaction with Novel Object

The duration of time spent with the novel object was not significantly predicted by location (χ^2_5 = 10.55, p= 0.071), sex (χ^2_1 = 1.92, p= 0.166) and by replicate number (χ^2_2 = 1.29, p= 0.521). Even though individuals spent an equal amount of time interacting with the object in all 6 populations, individuals in both the Joburg Public and Hidden enclosures spent the more time interacting with the novel object. Individuals in the WOB and Monte Right enclosures spent the smallest time interacting with the novel object (Figure 35).

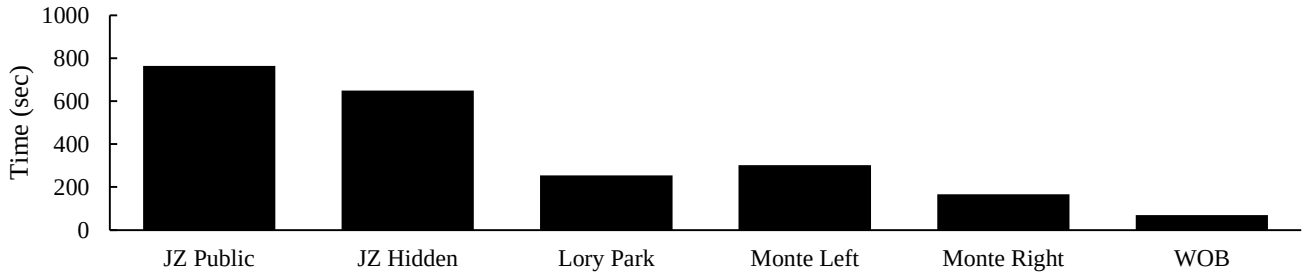


Figure 35: The time spent by ground hornbills interacting with the novel object in the 6 locations



Figure 36: The time spent by ground hornbills interacting with the novel object in the two sexes

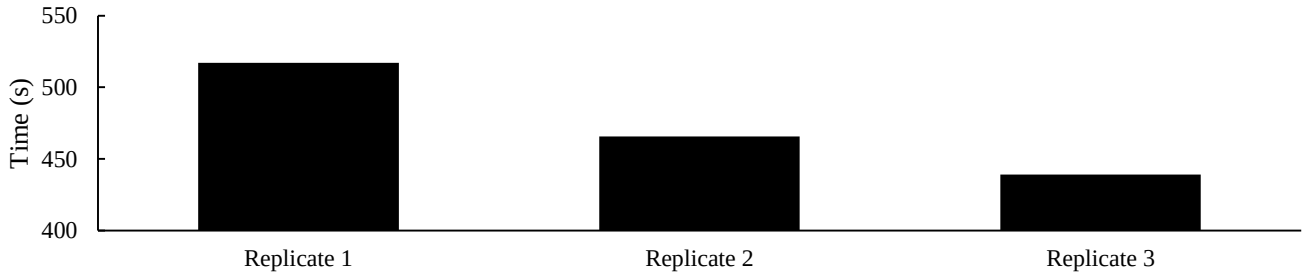


Figure 37: The time spent by ground hornbills interacting with the novel object in three replicates observations

Individual Differences

The three individuals in Johannesburg Zoo Hidden Enclosure differed significantly in their time spent interacting with the novel object (χ_4^2 = 33.37, p< 0.001; Figure 38). Male (Green) showed the longest interaction with the novel object in all 3 replicates, and the other male (Silver) showed the lowest interaction in replicate 1 (contribution to chi-squared analysis; Figure 38).

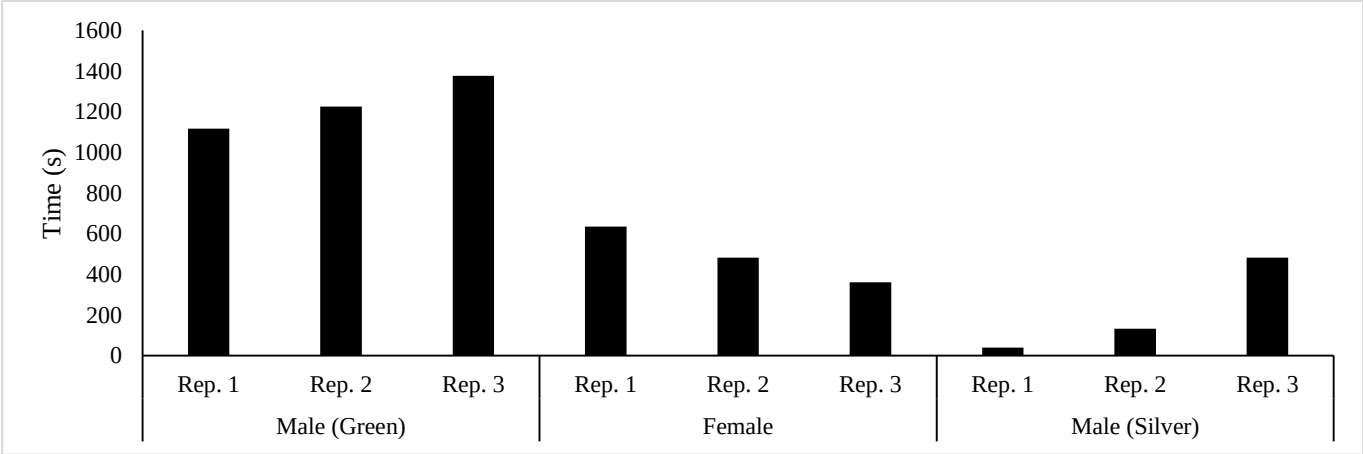


Figure 38: The time spent with the novel object by the three individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates (Rep).

The three individuals in the Joburg Zoo Public Enclosure showed a significant difference in their interaction with the novel object (χ_4^2 = 33, 37, p< 0.001; Figure 39). One male (Silver) showed a consistent shorter time spent with the novel object (contribution to chi-squared analysis; Figure 39).

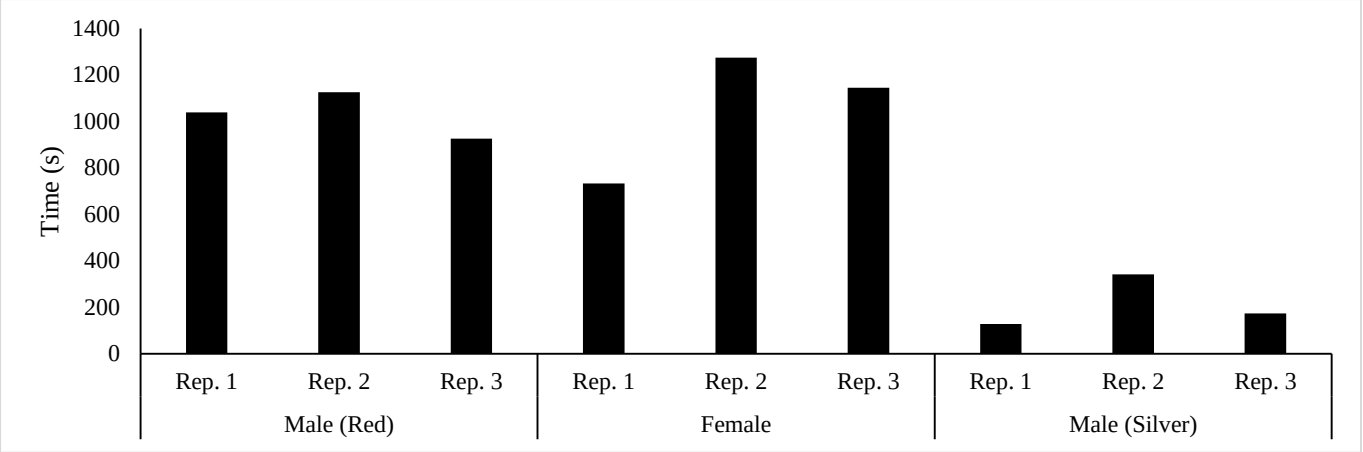


Figure 39: The time spent with the novel object by the three individual ground hornbills at the Johannesburg Zoo Public Enclosure in three replicates (Rep).

There was no significant difference in the time spent with the novel object between the two birds in Monte Casino Bird Gardens Right Enclosure (χ_2^2 = 2.82, p = 0.243; Figure 40). In contrast, in the Monte Casino Bird Gardens Left Enclosure, the two birds differed significantly in their time spent with the novel object (χ_2^2 = 13.11, p= 0.001; Figure 41). The male spent more time with the novel object in replicate 1 (contribution to chi-squared analysis; Figure 41).

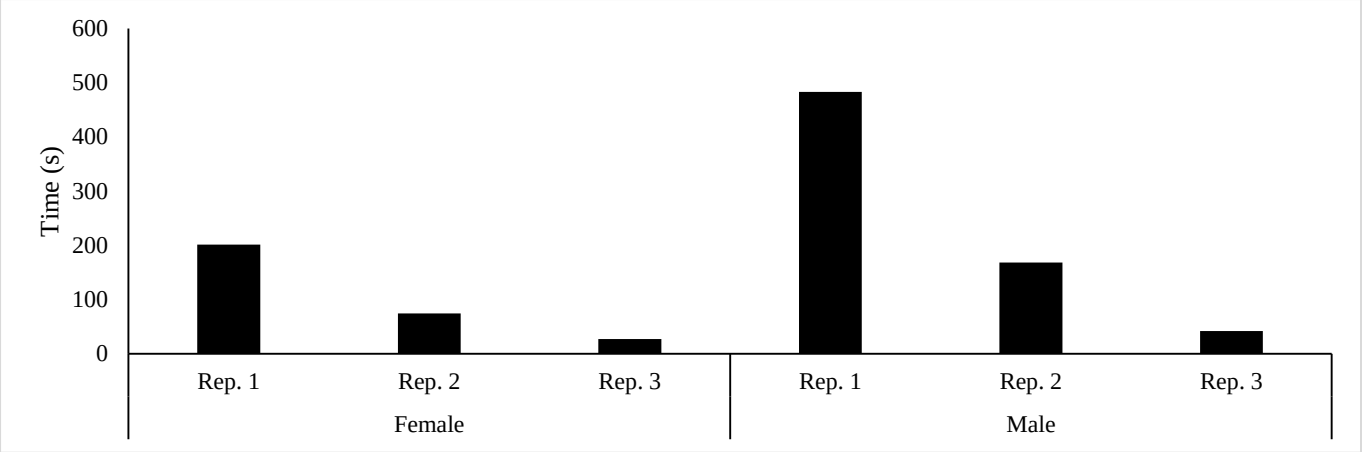


Figure 40: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates (Rep).

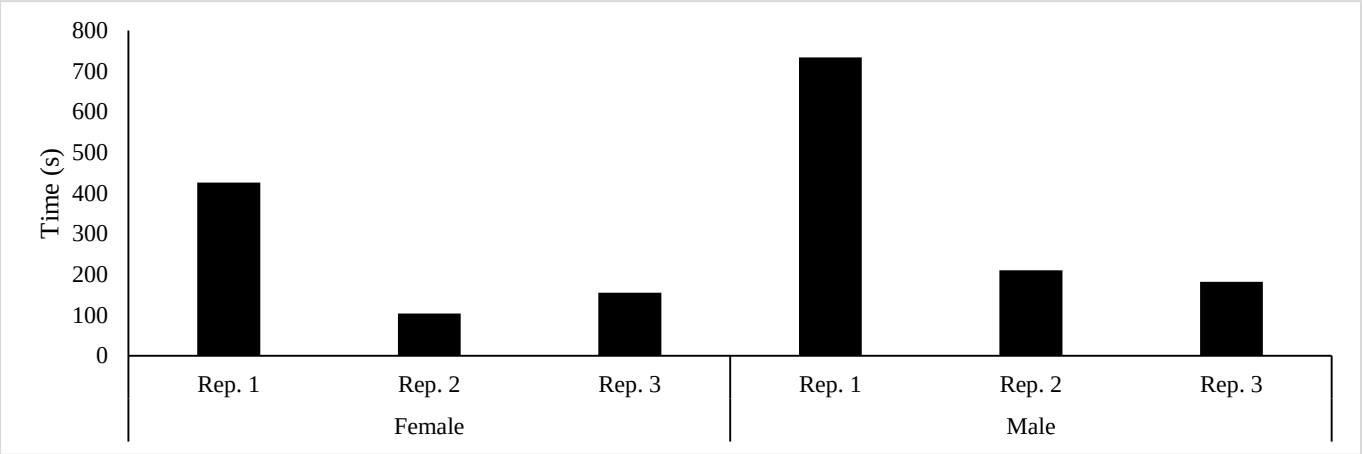


Figure 41: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates

In Lory Park, the two ground hornbills differed significantly in the time spent with the novel object (χ_2^2 = 45.44, p<0.001; Figure 42). The female spent more time with the novel object than the male in all 3 replicates (contribution to chi-squared analysis; Figure 42).

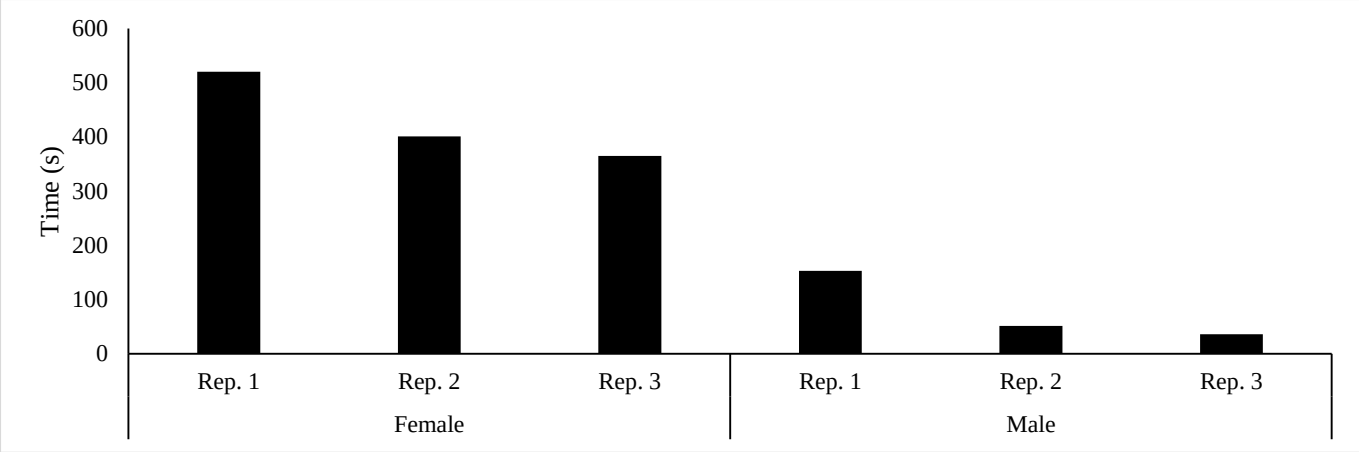


Figure 42: The time spent with the novel object by the two individual ground hornbills at the Johannesburg Zoo Hidden Enclosure in three replicates

In the World of Birds, all six individuals did not interact with the novel object, so no analyses were conducted.

The behavioural syndrome in captive ground hornbills

Behavioural syndromes among individual ground hornbill individuals were investigated by pairwise correlations between the variables scored in the general behavioural observations, sociality observations, space use observations and risk taking behaviour tests. Out of a total of 78 possible correlations, there were 19 significant correlations, 11 positive correlations and 8 negative correlations between the variables (with $r > 0.5$). The significant correlations mentioned above were syndromic (Mackay 2017).

Bolder individuals displayed behaviours that correlated with a shorter latency to approach novelty, quicker recovery after a startle, longer time spent interacting with the object, a longer time feeding and interacting with their beak, as well as greater vocalising, a larger amount of space used in the enclosure and a greater locomotion frequency. Less bold individuals displayed behaviours that correlated with the opposite to that of bold individuals, and had a longer latency to approach novelty, long recovery time after a startle, a shorter time spent interacting with the object, a shorter time feeding and interacting with their beak, as well as low vocalization and less amount of space used in the enclosure and the less they locomoted.

Table 21: The correlations between the variables scored in the general behaviours observations, sociality observations, space use observations and risk taking behaviour tests for 18 ground hornbill individuals (except space use for WOB individuals).

	Novel Interaction	**Novel Latency**	**Startle Test**	**Space Use**	**Feed**	**Perch**	**Social**	**Vocal**	**Preen**	**Lie down**	**Locomote**	**Interact**	**Thermo - regulation**
Novel Interact	*	0.28, 0.269	-0.35, 0.262	0.47, 0.122	0.62, 0.006	-0.34, 0.166	-0.23, 0.365	-0.57, 0.015	-0.34, 0.170		0.41, 0.093	0.66, 0.003	0.27, 0.286
Novel Latency		*	0.44, 0.148	0.10, 0.760	0.56, 0.016	-0.23, 0.360	-0.38, 0.124	-0.16, 0.534	-0.31, 0.206	-0.08, 0.755	0.29, 0.247	0.29, 0.247	-0.06, 0.823
Startle Tet			*	-0.41, 0.183	-0.05, 0.882	-0.02, 0.95	-0.37, 0.234	0.60, 0.040	-0.49, 0.103	0.36, 0.258	-0.04, 0.903	-0.15, 0.636	-0.09, 0.786
Space Use				*	0.55, 0.064	-0.76, 0.005	0.67, 0.017	-0.35, 0.260	0.32, 0.311	-0.58, 0.050	0.60, 0.039	0.58, 0.047	0.37, 0.241
Feed					*	-0.44, 0.068	-0.12, 0.624	-0.52, 0.027	-0.13, 0.603	-0.49, 0.035	0.30, 0.223	0.56, 0.015	0.06, 0.794
Perch						*	-0.13, 0.607	0.22, 0.384	-0.04, 0.872	0.34, 0.167	-0.66, 0.003	-0.61, 0.008	-0.38, 0.119
Social							*	0.39, 0.112	0.83, < 0.0001	0.03, 0.904	-0.46, 0.053	-0.46, 0.056	0.49, 0.041
Vocal								*	0.26, 0.292	0.44, 0.065	-0.43, 0.075	-0.56, 0.016	-0.02, 0.932
Preen									*	0.01, 0.988	-0.53, 0.024	-0.51, 0.032	0.50, 0.034
Lie down										*	-0.38, 0.117	-0.52, 0.026	-0.11, 0.669
Locomote											*	0.72 0.001	-0.16, 0.512
Interact												*	0.12, 0.633
Thermo - regulation													*

DISCUSSION

I investigated the inter-individual behavioural variation in the threatened Southern Ground Hornbill. Specifically, I documented the behaviour of individual captive ground hornbills housed in four institutions (6 population groups) in South Africa. These ground hornbills were either captive hatched or rescued birds, housed in pairs or small flocks (up to 6 individuals). I additionally assessed whether the ground hornbills had personalities and behavioural syndromes, and whether there were sex and institution related behavioural differences. I discuss my findings in each of my six objectives, below.

The broad behavioural categories of captive ground hornbills

I generated a written and video ethogram of nine broad behavioural categories (namely perching, locomotion, object interaction, lying down, social interaction, preening, feeding, thermoregulation and vocalising) of the captive ground hornbills. Overall, the behaviours that were observed in the captive populations in this study were a good representation of the behaviours also seen in the free-living populations (Kemp and Kemp 1980) as well as in another captive study of the species (Cooper and Jordan 2013). My categorisation of behaviours can be used for future research by ground hornbill handlers and even the public to understand the general behaviours displayed by individual ground hornbills.

The diurnal activity patterns of captive ground hornbills

The second objective of my study was to document the diurnal activity patterns of ground hornbills in a captive environment. Free-living ground hornbills have a bimodal activity profile where activity decreases towards midday (when the groups spends time resting) and then increases again later in the day (Kemp and Kemp 1980). I predicted that the activity profile of the captive ground hornbill would be similar to that of their free-living counterparts. However, the patterns of the captive ground hornbills in all enclosures combined did not conform to the bimodal pattern of their free-living counterparts, but rather their activity, at least for the three common behaviours (perching, locomotion, object interaction), remained fairly constant throughout the sampling time.

I found that perching occupied a quarter of the time among all ground hornbills studied. Locomotion, object interaction, and lying down occupied greater than 10% of the bird's time; the remaining behaviours occurred less frequently.

Kemp and Kemp (1980) found that free-living ground hornbills' activity varied from day to day, with the group's activity mostly consisting of movement from roosts, movement along territorial boundaries, movement to and from feeding areas, as well chasing neighbouring group members. Similarly, locomotion occurred frequently in my study of captive hornbills.

The higher level of perching behaviour in my study compared to free-living ground hornbills might indicate a reduced need to forage and defend territories. Similarly, orangutans *Pongo pygmaeus*, showed reduced overall low activity in captivity compared to nature, with the orangutan's activity being reduced by the smaller usable surface area, reduced number of movable objects, as well as regular food availability (Perkins 1992). In another example, a comparison of individual behaviour between captivity and the free-living blue tits *Cyanistes caeruleus,* showed lower activity levels, exploratory tendency and neophobia in captive birds (Herborn *et al.* 2010).

In the only other known study done on the activity of captive ground hornbills, Cooper and Jordan (2013) investigated the random (i.e. irregular sampling regime vs daily sampling) time-activity budgets of captive ground hornbills at the Johannesburg Zoo. They found that there were differences in activity and behaviours observed in captivity compared to the free-living ground hornbills studied by Kemp and Begg (2001). The captive ground hornbills, did not need to forage, defend territories nor did they have long distances to travel and did not show a bimodal activity profile (Cooper and Jordan 2013). Therefore, the constant (non-bimodal) overall activity pattern seen in the ground hornbills in both my study and in that of Cooper and Jordan (2013) could suggest a captive phenomenon, in which behaviours are modified. This implies that the bimodal activity of the ground hornbill is not a fixed circadian activity (except for possibly diurnal activity). Animals have been known to alter their bimodal circadian rhythm in nature to unimodal in captivity. For example, Gattermann *et al.* (2008) found that the mechanisms controlling circadian rhythms in golden hamsters *Mesocricetus auratus* were altered in a laboratory setting from a strictly diurnal profile in nature to an extended diurnal and nocturnal profile in captivity.

Comparisons between institutions showed that there were significant differences in five (feeding, perching, social, vocalization, thermoregulatory behaviour) out of the nine behaviours displayed by the captive ground hornbill individuals in the six different populations. These results indicate differences in the husbandry routine and/or the enclosure object composition. For example, a reason for population differences in feeding behaviour

could be a result of a different feeding routine and different dietary composition. Individuals in the Joburg Public display showed the highest feeding frequency among the other five populations, with the Lory Park individuals having the lowest feeding frequency.

A reason for the difference in perching and thermoregulation could be due to the different number of trees, shade cloths and perches present in the enclosure. In particular, individuals in the Monte Right and Left enclosures had the highest perching frequency followed by Lory Park. These three locations were the smallest enclosures and the low perching might be because the space available for locomotion was reduced in the small spaces. In contrast, the lowest perching frequency was observed in the Joburg Hidden and public displays which both had large volume enclosures, enabling locomotion.

The WOB had the greatest social interaction frequency compared to the other populations. A reason for the high social interactions could be a result of the population having the highest number of individuals present (6 individuals), as well as having juvenile individuals that naturally play or compete for dominance. Monte Left and Right enclosures and the Lory Park enclosures had the lowest social interactions and all three comprised of a breeding pair.

Location was not a significant predictor of preening, lying down, locomotion, nor interactions with objects. These natural maintenance behaviours are thus conserved across populations and not affected by routine nor enclosure size and composition. Out of the nine behaviours, there was only a sex effect in the locomotion, with females' locomoting significantly less than males, suggesting that males were generally more active in captive environments. A reason for the sex differences in locomotion could be that males do more territorial patrolling than females (Kemp and Kemp 1980).

The transactional (two-way social) interactions of captive ground hornbills

Ground hornbills have a complex intragroup social organisation, and an elaborate territorial maintenance behaviour (Kemp and Kemp 1980), and little is known about whether individuals within groups behave differently than between groups. The six captive populations in this study were already well established prior to any observations. Therefore, I predicted that there would be a higher frequency of amicable behaviour than aggressive behaviour. In support, aggression was scored only in the Johannesburg Hidden and the World of Birds populations, and virtually absent in the other populations; due to the large number of zeros for aggressive interactions, socio-metric analyses could not be run on the results for the

Johannesburg Zoo public display, Lory Park, as well as Monte Casino Bird Gardens Right and Left enclosures. The socio-metric analyses showed that three populations (Lory Park and the two Monte Casino garden groups) showed significantly high reciprocal amicable interactions. All three had a couple – a male and female only. A reason for the high amicability could be due to the mating and courtship, as suggested by Kemp and Kemp (1986).

Extensive research has been done on the captive behaviours of different animals and how they avoid aggression in restricted space (deWaal, 1989; deWaal *et al.*, 2000). Chimpanzees cope with restricted space by using tension-reduction tactics and conflict-avoidance tactics to limit aggression (Duncan *et al.*, 2013). The reduced aggression in the studied populations could suggest that the ground hornbill individuals were using a conflict-avoidance tactic in established groups. The WOB was the only population of the six to show a significant aggression occurrence, that between the two juveniles. The WOB population was the largest group in this study, consisting of six individuals, an alpha male and an alpha female and four of their offspring. The social interactions of the WOB ground hornbills suggest a tightknit family unit and the aggressive behaviour between the two juveniles could be a result of either dominance behaviours testing or just rough play.

The space use and exploratory behaviour of captive ground hornbills

Free-living ground hornbills' groups fly from their tree roosts at first light and thereafter spend most of their day on the ground where foraging was the main activity (Kemp and Kemp 1986). I therefore predicted that ground hornbill would spend the majority of their time in areas of the enclosure that have feeding stations, large perches or trees and nest boxes. The space use varied between the individuals in the different institutions, but overall the individuals spent more time in areas with large perching platforms, areas with a nest box and a small river stream as well as areas that consisted of a boundary fence.

When comparing the space use of each individual within an enclosure, the results showed that there was a distinct overlap among the individuals. In the Joburg Hidden enclosure, three individual ground hornbills all overlapped in their use of five of the 12 zones. In the Joburg Public enclosure, the three individual ground hornbills all overlapped in five of the 12 zones. In the Monte right enclosure, individuals overlapped in five of the 12 zones. In the Monte left enclosure, individuals overlapped in three of the 12 zones. In the Lory Park enclosure,

individuals overlapped in four of the 12 zones. In these cases, on numerous occasions, the individuals were using the same zones at the same time. The most common zones that were used contained either the entrance gate, the feeding station, boundary fence closest to the foot traffic of people, a perch platform or a zone that had constant shade from the large tree.

The risk-taking behaviour of captive ground hornbills in their responses to novelty and a startle

An individual's behaviour is influenced by the interaction between its genes and the environment that it inhabits (Fuller *et al*. 2005). Therefore, it is possible for individuals in different populations of the same species to behave differently in a way that maximises their fitness for the different environments they occupy (Taylor 1991). To establish whether captive ground hornbills differed in their risk taking and neophobic responses in each enclosure, I used two well-known personality tests, namely startle tests and novel object tests. I predicted that individuals and sexes would differ in their risk-taking behaviour in the different institutions.

The results from the startle tests showed that individual behaviour did not differ among the ground hornbills in the six populations, did not differ between sexes nor did it differ in the 3 replicates. However, in the novel object test, individual boldness was influenced by location and replicate number. Overall the individuals in Lory Park enclosure took the longest time to return to normal activity, followed by WOB, Joburg Hidden enclosure and Monte Left enclosure.

Individuals in Lory Park and WOB were overall more "timid" than the others for the novel object. The reasons for this could be due to the fact that they were unaccustomed to novelty. For example they received less enrichment than the other individuals in the other institutions. Another aspect to consider, particularly with the WOB individuals, is that their responses could be because they reacted as a group to the novelty, such that all individuals were influenced similarly by the novel object (i.e. a behavioural contagion).

Risk taking behaviour tests were conducted in three replicates per session per ground hornbill population. The latency to resume normal activity in the three replicates was similar with a slightly greater response in replicate 2. Generally, the latency to touch (and continue to interact with) was greater in replicate 1 compared to replicate 3, which shows habituation to the novel object. Similarly, Eastern chipmunks *Tamias striatus* showed habituation and

behavioural carryover in activity/exploration and docility across replicates in risk taking behaviour (Martin and Réale 2008). The duration of time spent with the novel object was not significantly predicted by replicate number.

Both personality tests showed that there was no sex effect, and ground hornbill personality did not differ among males or females within a group, contrary to my prediction. Similarly, Patrick and Weimerskirch (2014) studied personality in black browed albatross *Thalassarche melanophris* and found that there were no sex effects on boldness. In another example, Brust *et al.* (2014) found no sex effect in personality of zebra finches *Taeniopygia guttata,* and found no sex effect in the measured personality traits.

Comparisons between individuals in each population separately revealed inconsistent individual and replicate variation. One reason for the variation between individuals could be due to individuals responding collectively as part of socially mediated responses (e.g. local enhancement behavioural contagion) vs individual responses. In contrast, for the novel object tests, there were some consistent individual responses, indicative of personality differences. In particular, the female in the Monte Casino Bird Gardens Right population showed consistently greater latency to approach than the male, whereas the male at the Lory Park population took consistently shorter time to approach the novel object than the female. In the Johannesburg Zoo Hidden population, one male showed consistently longer interaction with the novel object and one male in the Johannesburg Zoo Public population showed consistent lower time spent with the novel object. Finally, in the Lory Park population, the female spent more time with the novel object than the male.

The behavioural syndrome in captive ground hornbills

Using the data from objectives 1-5, I tested whether a behavioural syndrome exists in ground hornbills. I ran correlations on functionally different behaviours for 18 individuals combined (excluding only space use from the six the individuals in WOB). Out of a total of 78 possible correlations, there were 19 significant correlations, 11 positive correlations and 8 negative correlations between the variables (with $r > 0.5$). These correlations where indicative of a syndrome (i.e. consistent behavioural responses across contexts; Sih *et al*. 2004a; Bell and Stamps 2004).

CONCLUSION

I aimed to investigate the behaviour of individual captive ground hornbills housed in different institutions in South Africa. Mine is the first study to consider individual variation in the behaviour of the species. Overall, the six populations showed differences as well as similarities in nine behaviours considered here. The similarities in activity patterns of ground hornbills in the populations suggest that all birds have adapted to the optimal conditions in captivity, which reduces their need to forage. The low levels of aggression could be because the birds have already established settled groups. Another reason for the low aggression is the fact that human minders keep only non-aggressive birds together (Anderson *et al.* 2002). When looking at the individual differences among the birds, the low differences in risk taking could be because captive birds are accustomed to loud noises such as car hooters, screaming children and general loud ambient noises from urban life. Since I was unable to isolate the birds during tests, another reason for the low individual differences in risk taking behaviour could be that they are making decisions as a group (local enhancement, behavioural contagion). Overall, through observation and quantifying of behaviours, I conclude that the behaviours of the 18 captive birds showed a behavioural syndrome, in that behaviours were correlated in bold and less bold individuals.

Conservation relevance

There have been some studies done on ground hornbills (Kemp and Kemp 1980; Theron 2011; Cooper and Jordan 2013; Kemp 2017), all of which have contributed significantly to the overall understanding of ground hornbill biology. Even though Cooper and Jordan (2013) also considered the time-activity budgets in captive ground hornbills, they did not study the behaviour of individual ground hornbills. Therefore, nothing is known about the ground hornbill's individual behaviour and whether they have personalities and behavioural syndromes. Thus, the knowledge of the behaviour of individuals and how it differs in different contexts could be beneficial for general captive handling and husbandry as well as for future reintroductions, by identifying suitable individuals to form pairs and social groups. These findings allow for a greater understanding of the individual differences in captive ground hornbills, which are important when considering how individuals are managed and respond to interactions with other conspecifics in captivity and for the inclusion in future release programmes.

Understanding animal behaviour is fundamental to animal conservation, as it allows for the correct formation of groups and the correct reintroduction strategies (for example release the individuals in groups, pairs or alone). Previous research has shown that both wild and captive animal populations show rapid changes in behaviour as a consequence of conservation attempts (Marliave *et al*. 1993; Trut, 1999; Drent *et al.*, 2003). These changes in behaviour can affect the success of conservation strategies, and therefore understanding individual behavioural differences can play an important role in conservation practices.

Future studies

For future studies I would suggest extending the research to more institutions, to account for different age and sex compositions. Perhaps, studying the behaviour of individuals from the initiation of group formation over time will show whether behaviours are shaped (and converges) by social learning, as assumed here. Another issue would be to develop a way to study risk taking behaviour by individuals, either by confining the individuals or studying them before they are placed in groups.

SUPPLEMENTARY GRAPHS

Perching

Johannesburg Zoo Hidden Enclosure

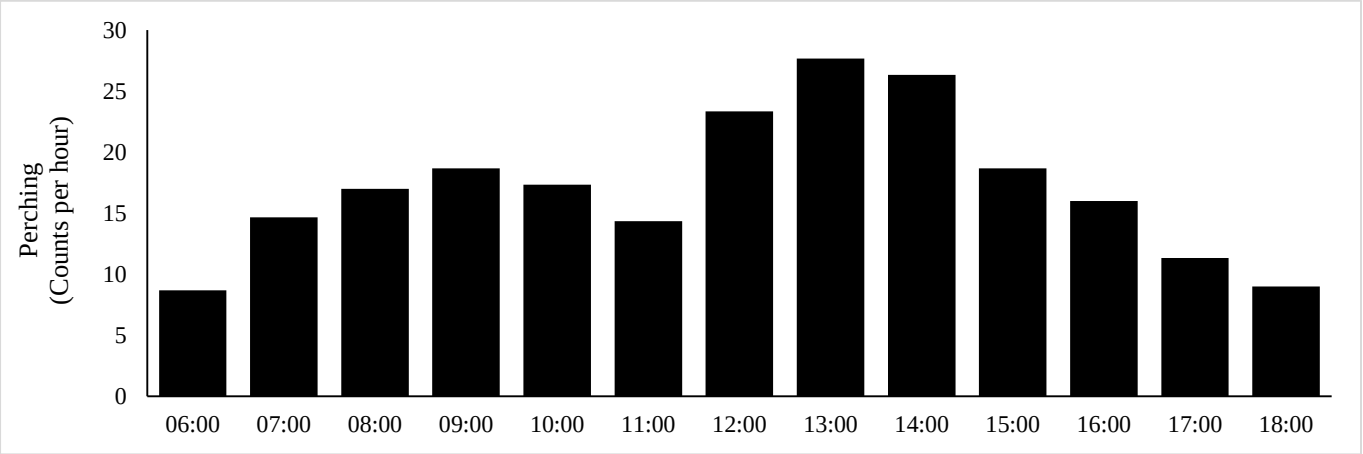


Figure 1S: The 12 hour activity-time profile of perching in three captive ground hornbills in the Johannesburg Zoo Hidden Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Johannesburg Zoo Public Enclosure

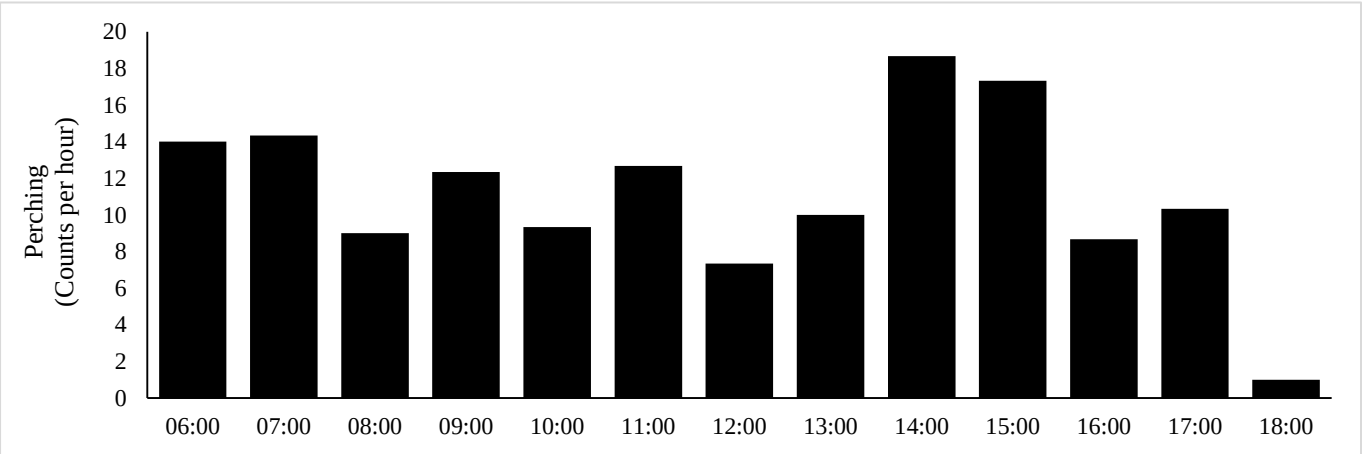


Figure 2S: The 12 hour activity-time profile of perching in three captive ground hornbills in the Johannesburg Zoo Public Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Left Enclosure

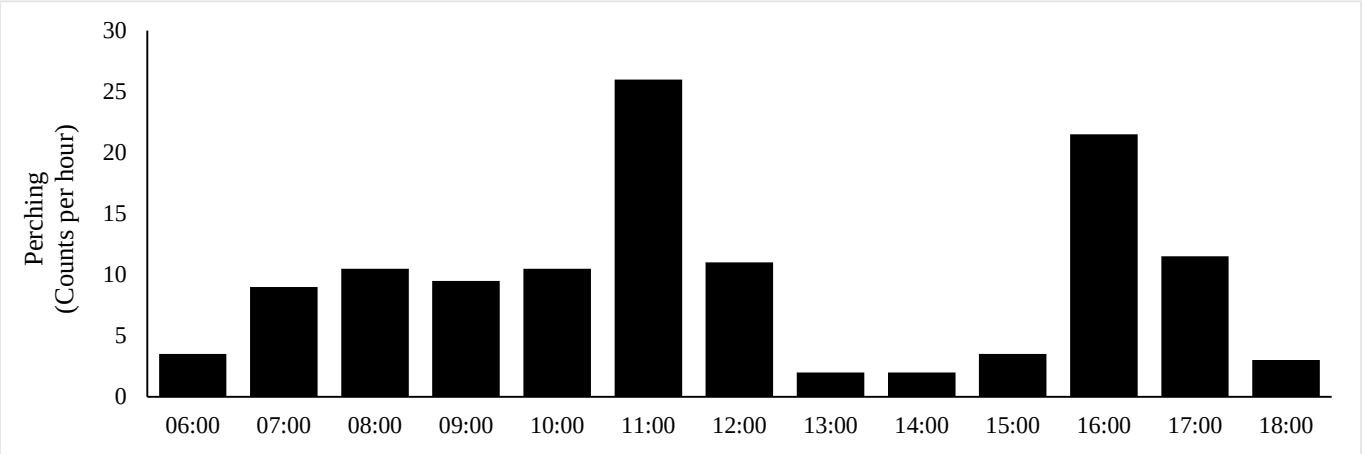


Figure 3S: The 12 hour activity-time profile of perching in two captive ground hornbills in the Monte Casino Left Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Right Enclosure

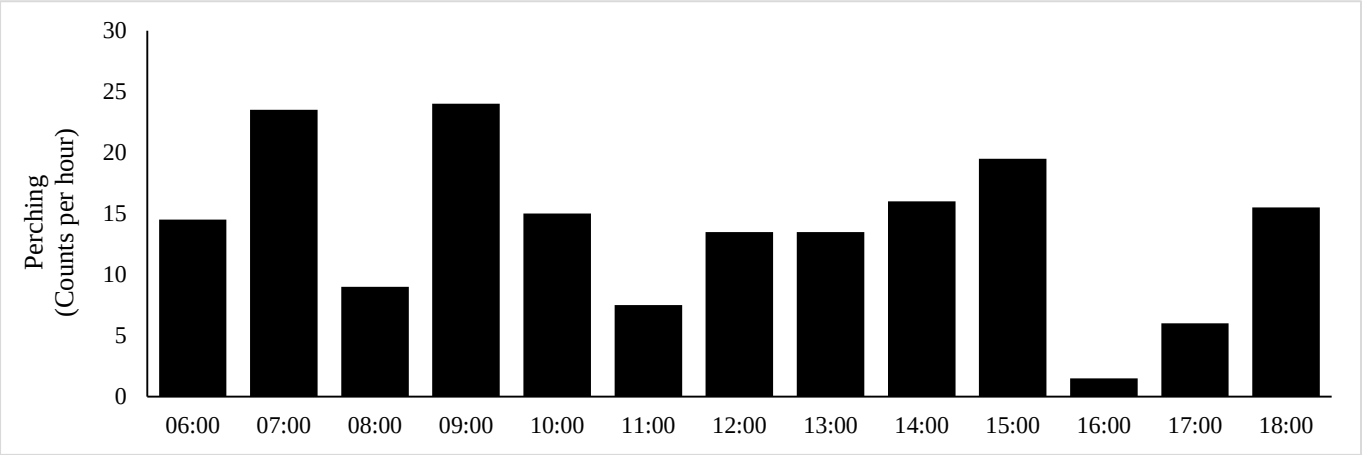


Figure 4S: The 12 hour activity-time profile of perching in two captive ground hornbills in the Monte Casino Right Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Lory Park Enclosure

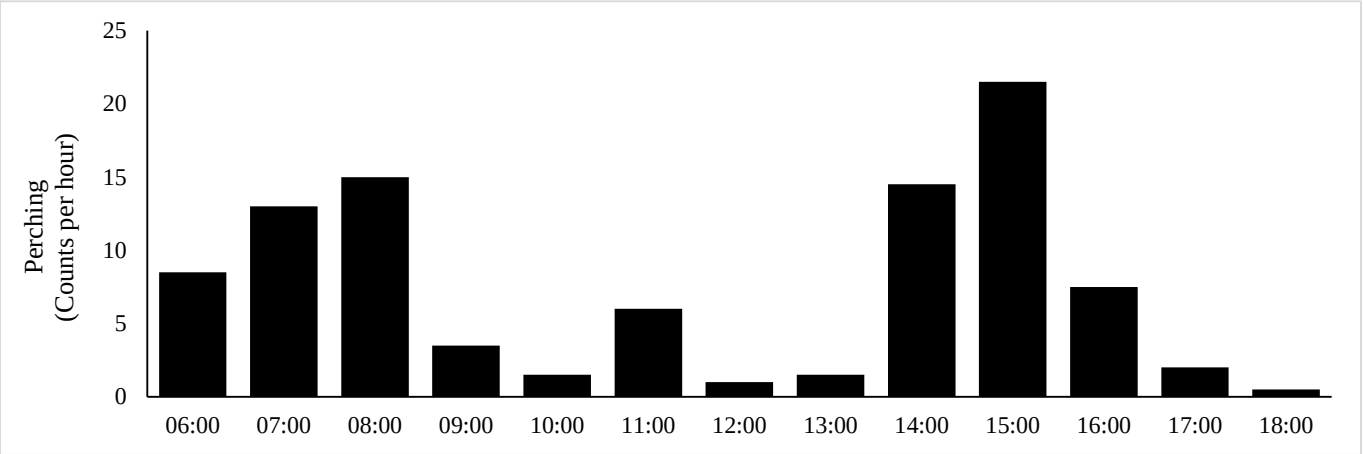


Figure 5S: The 12 hour activity-time profile of perching in two captive ground hornbills in the Lory Park Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

World of Birds Enclosure

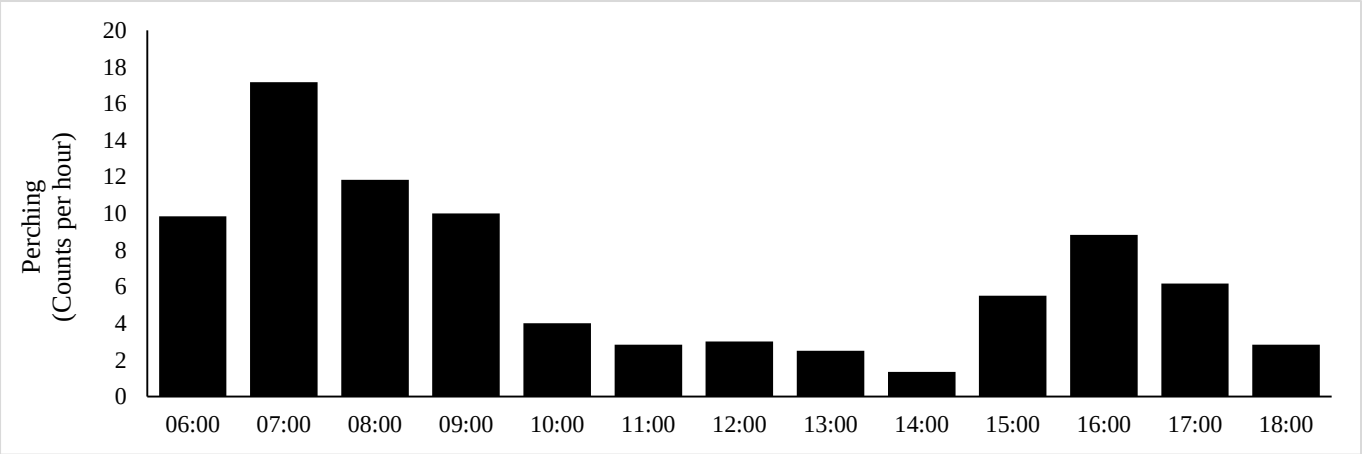


Figure 6S: The 12 hour activity-time profile of perching in six captive ground hornbills in the World of Birds Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Object Interaction

Johannesburg Zoo Hidden Enclosure

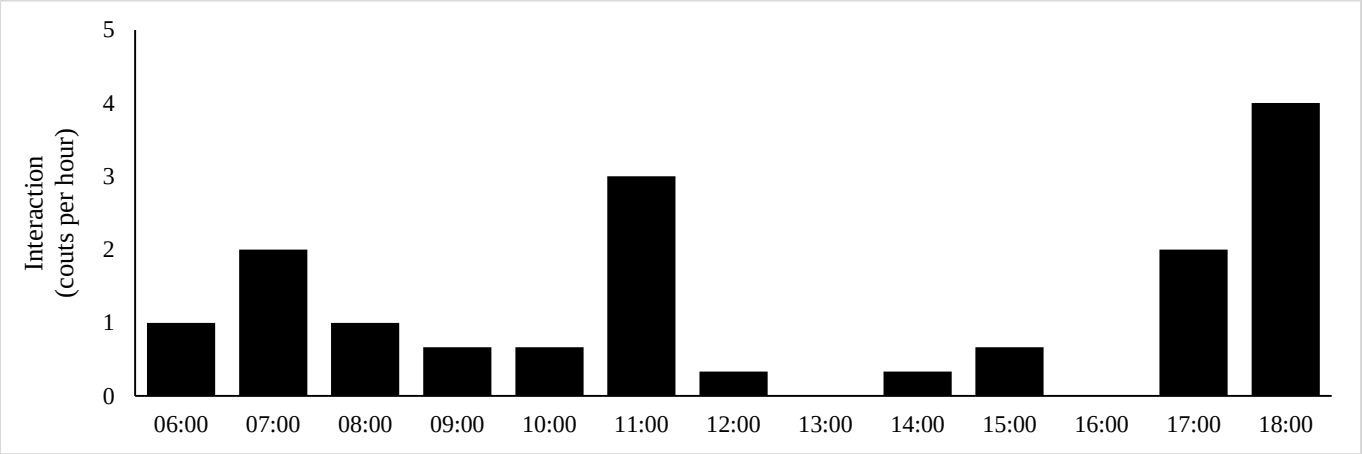


Figure 7S: The 12 hour activity-time profile of interaction in three captive ground hornbills in the Johannesburg Zoo Hidden Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Johannesburg Zoo Public Enclosure

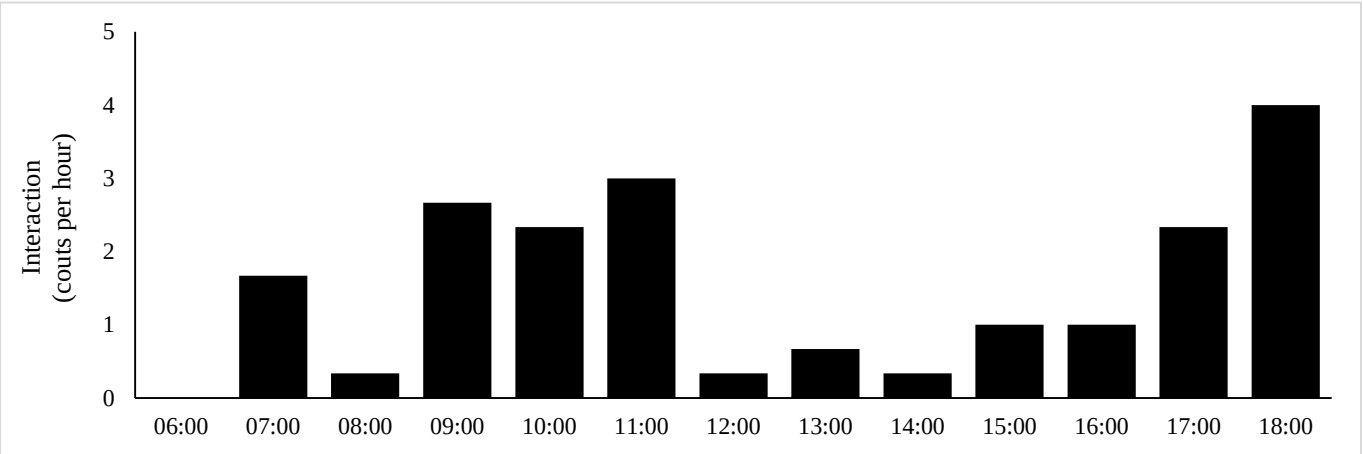


Figure 8S: The 12 hour activity-time profile of interaction in three captive ground hornbills in the Johannesburg Zoo Pulic Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Left Enclosure

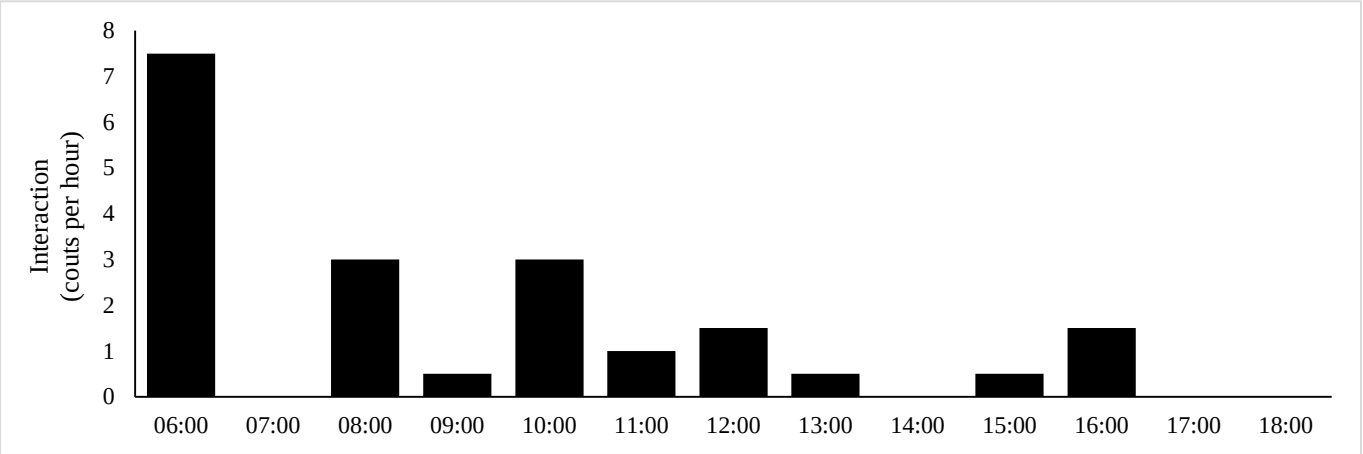


Figure 9S: The 12 hour activity-time profile of interaction in two captive ground hornbills in the Monte Casino Left Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Right Enclosure

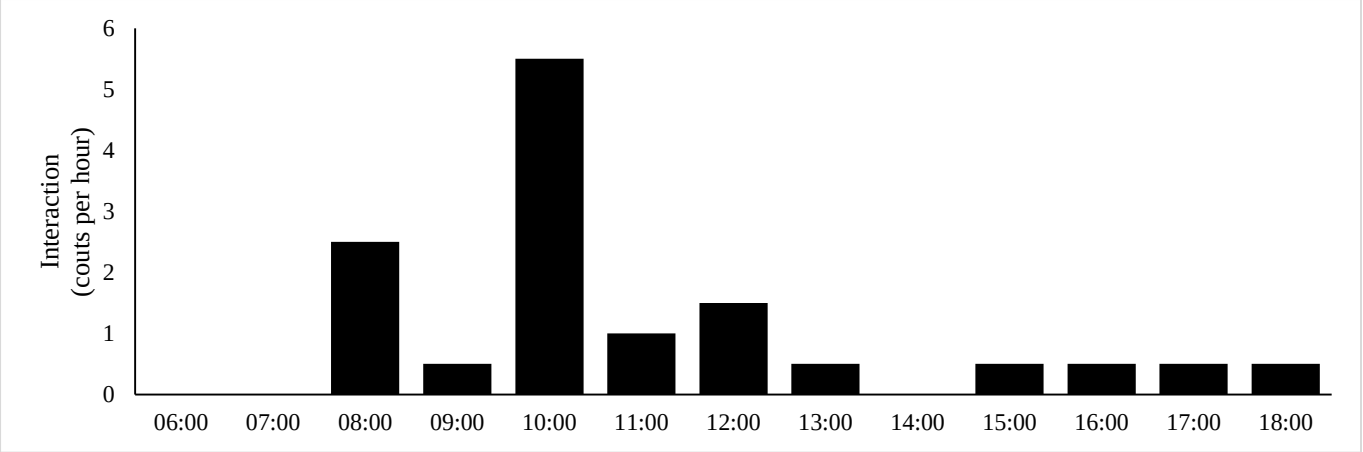


Figure 10S: The 12 hour activity-time profile of interaction in two captive ground hornbills in the Monte Casino Right Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Lory Park Enclosure

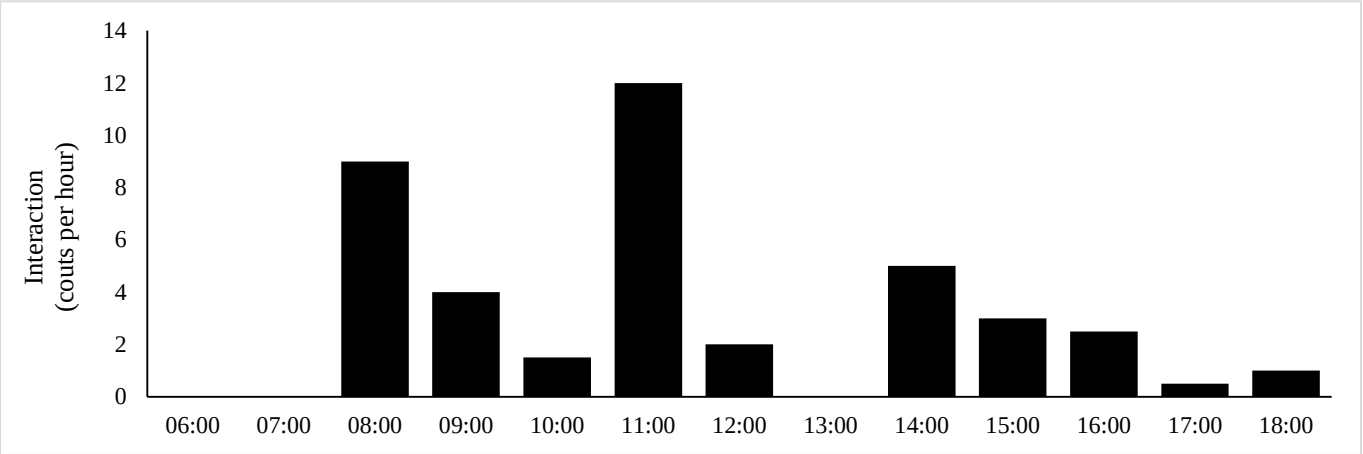


Figure 11S: The 12 hour activity-time profile of interaction in two captive ground hornbills in the Lory Park Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

World of Birds Enclosure

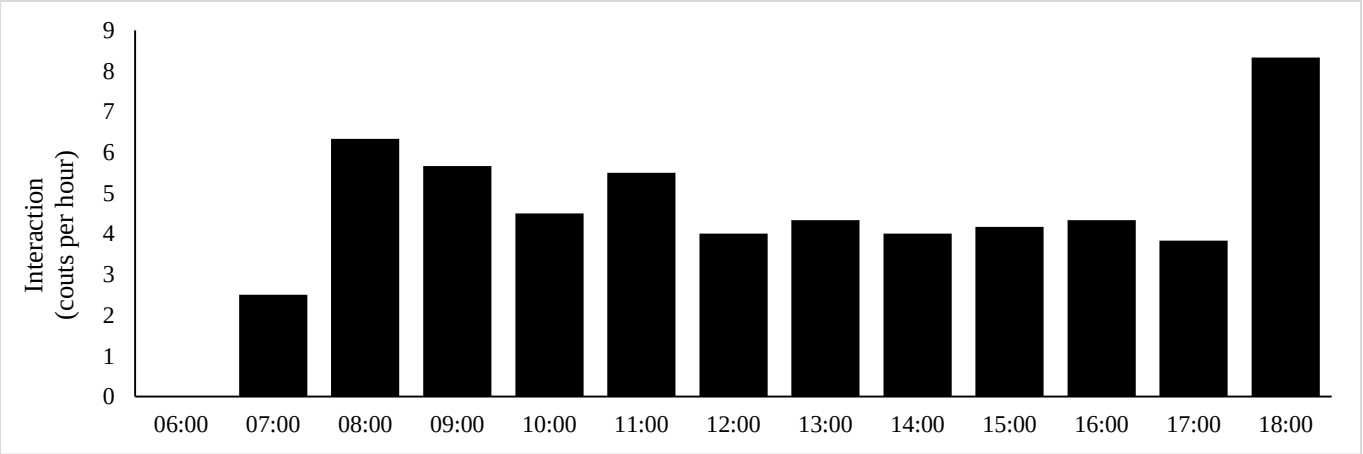


Figure 12S: The 12 hour activity-time profile of interaction in six captive ground hornbills in the World of Birds Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Locomotion

Johannesburg Zoo Hidden Enclosure

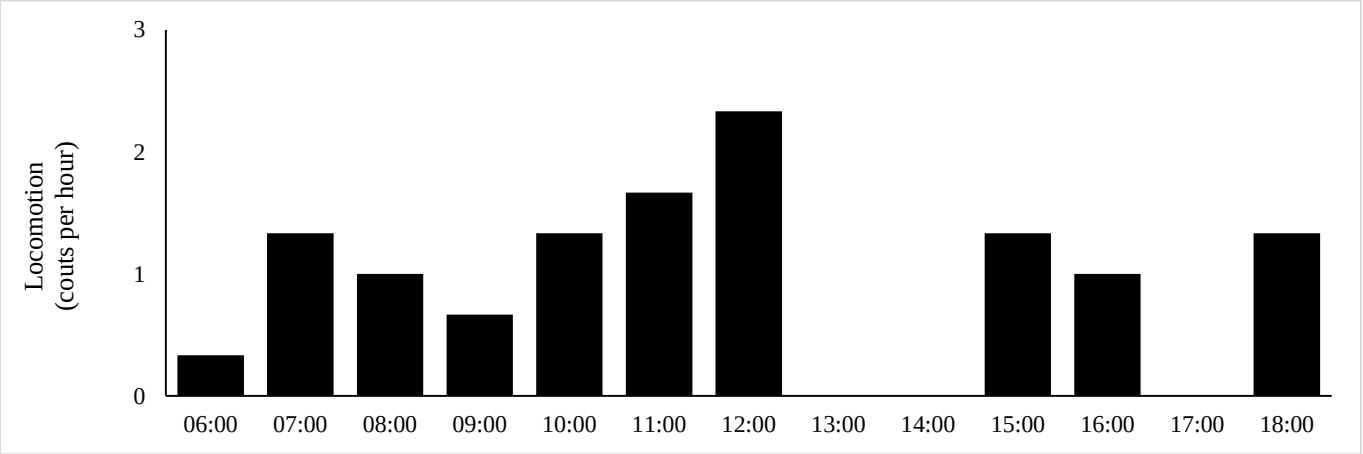


Figure 13S: The 12 hour activity-time profile of locomotion in three captive ground hornbills in the Johannesburg Zoo Hidden Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Johannesburg Zoo Public Enclosure

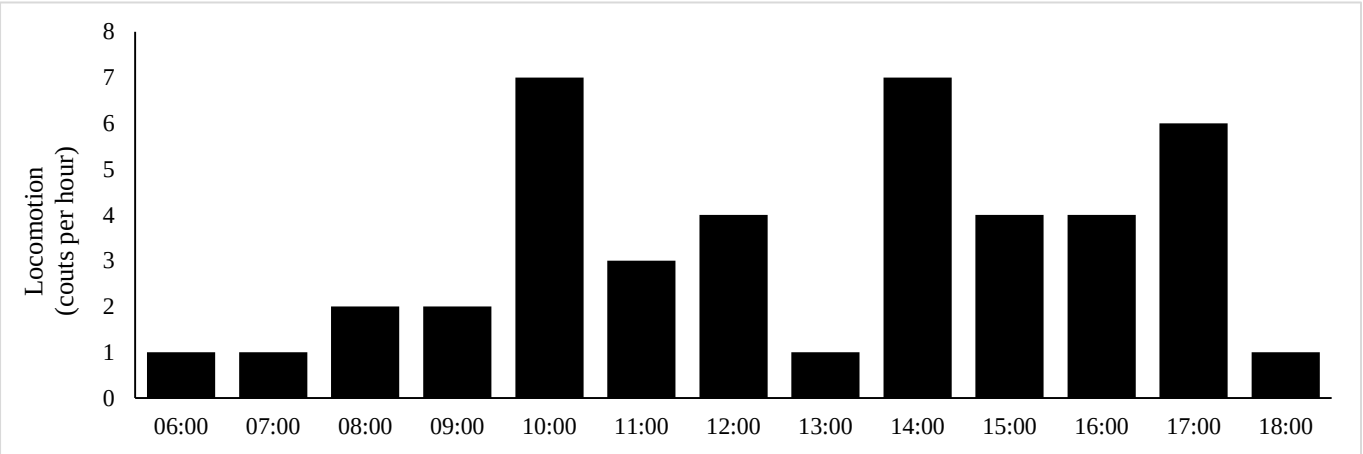


Figure 14S: The 12 hour activity-time profile of locomotion in three captive ground hornbills in the Johannesburg Zoo Public Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Left Enclosure

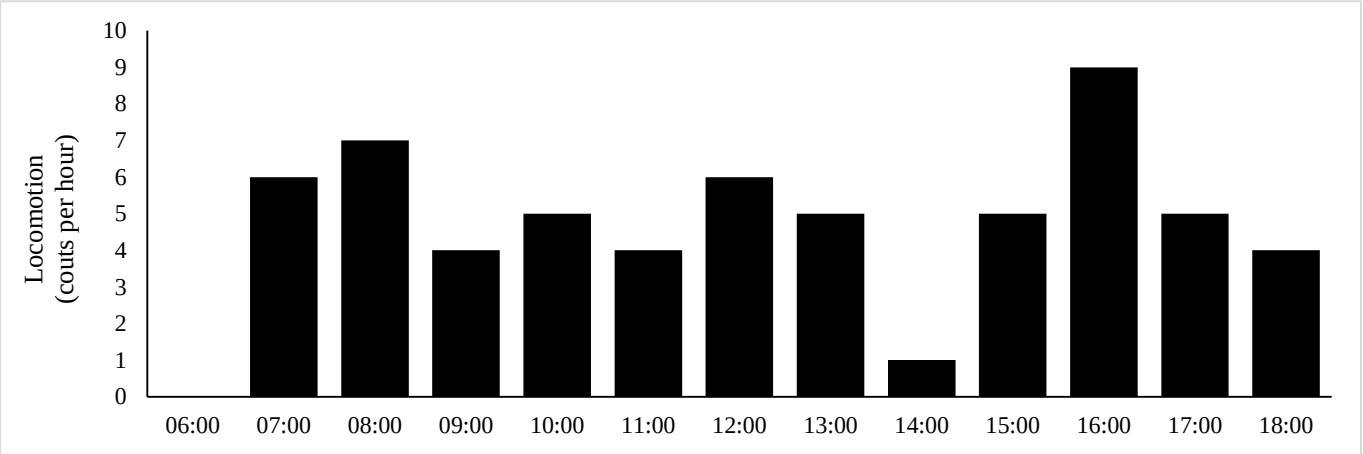


Figure 15S: The 12 hour activity-time profile of locomotion in two captive ground hornbills in the Monte Casino Left Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Monte Casino Right Enclosure

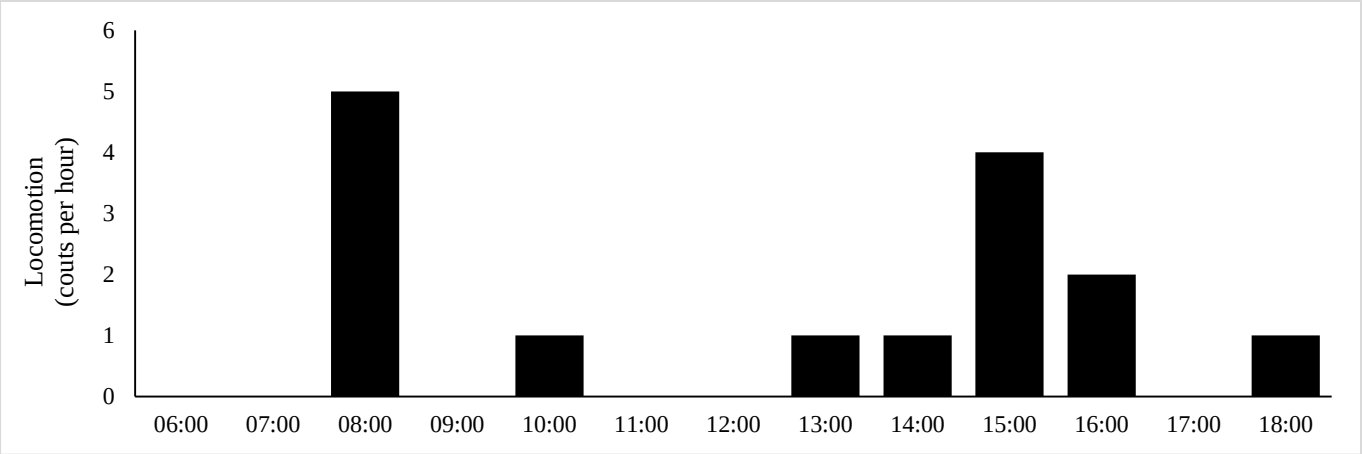


Figure 16S: The 12 hour activity-time profile of locomotion in two captive ground hornbills in the Monte Casino Right Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00.

Lory Park Enclosure

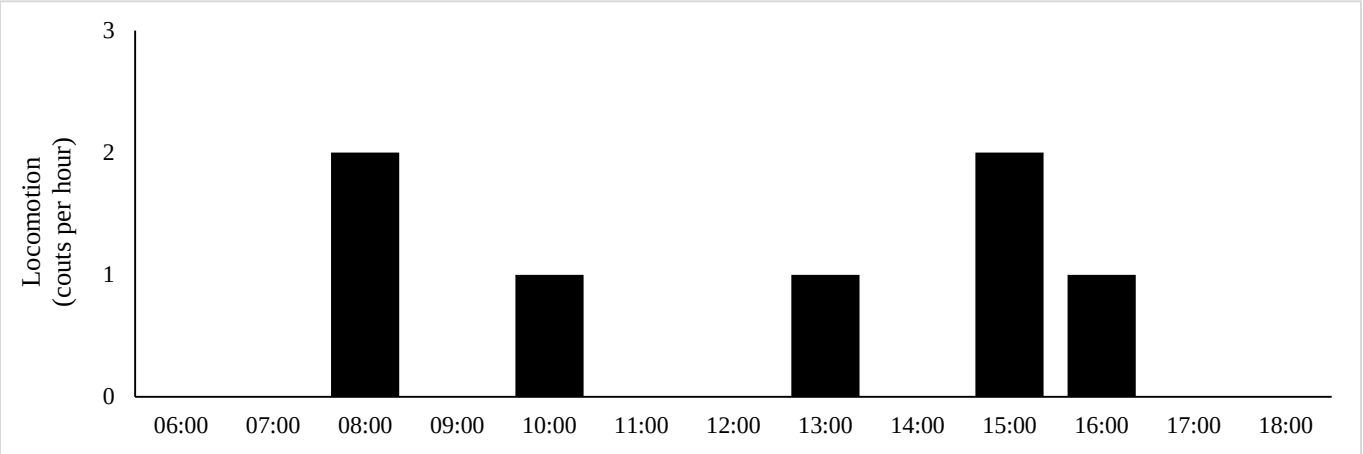


Figure 17S: The 12 hour activity-time profile of locomotion in two captive ground hornbills in the Lory Park Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00

World of Birds Enclosure

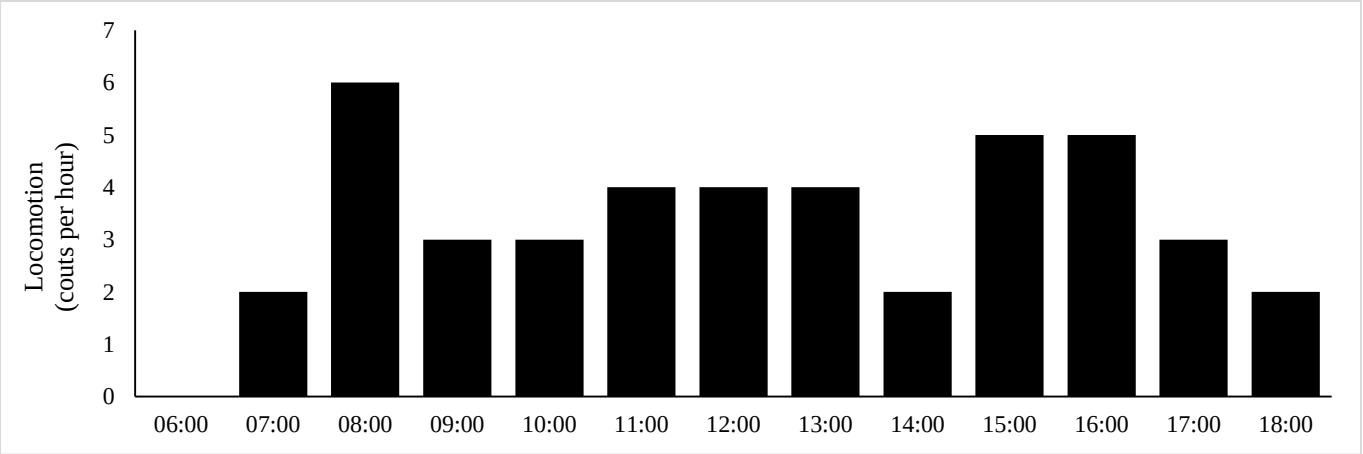


Figure 18S: The 12 hour activity-time profile of locomotion in two captive ground hornbills in the World of Birds Enclosure. Bars denote the counts per hour spent doing that particular activity. During the study period sunrise occurred between 06h00- 06h30 and sunset between 17h30-18h00

REFERENCES

Aguilar, R., Gil, L., Gray, J. A., Driscoll, P., Flint, J., Dawson, G. R. Giménez-Llort, L., Escorihuela, R. M., Fernandez-Teruel, A., and Tobeňa, A. 2003. Fearfulness and sex in F2 Roman rats: Males display more fear though both sexes share the same fearfulness traits. *Physiology and Behaviour* 78(4–5): 723-732.

Alexander, B. K., and Roth, E. M. 1971. The effects of acute crowding on aggressive behaviour of Japanese monkeys. *Behaviour* 39: 73–90.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 3-4.

Anderson, U. S., Benne, M., Bloomsmith, M. A., and Maple, T. L., 2002. Retreat space and human visitor density moderate undesirable behaviour in petting zoo animals. *Journal of Applied Animal Welfare Science* 5: 125–137.

Anderson, D. L., Fisher, K.M., and Norman, G. J. 2002. Development and evaluation of the conceptual inventory of natural selection. *Journal of research in Science Teaching* 39(10): 952-978.

Anderson, U. S., Kelling, A. S., Pressley-Keough, R., Bloomsmith, M. A., and Maple, T. L. 2003. Enhancing the zoo visitor's experience by public animal training and oral interpretation at an otter exhibit. *Environment and Behaviour* 35: 826–841.

Augustsson, H., and Meyerson, B. J. 2004. Exploration and risk assessment: a comparative study of male house mice (*Mus musculus*) and two laboratory strains. *Physiology and Behaviour* 81(4): 685-698.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1-48.

Bell, A. M., and Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* 68: 1339–1348.

Bell, A. M., and Sih A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology letters* **10**: 828–834.

Benjamini, Y., and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society* 57(1): 289-300.

Brent, L., Kessel, A. L., and Barrera, H. 1997. Evaluation of introduction procedures in captive chimpanzees. *Zoo Biology* 16: 335–342.

Briffa, M., Rundle, S. D. and Fryer, A. 2008. Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences* 275: 1305-1311.

Broms, K. M., Johnson, D. S., Altwegg, R., and Conquest, L. L. 2014. Spatial occupancy models applied to atlas data show Southern Ground Hornbills strongly depend on protected areas. *Ecological Applications* 24(2): 363-374.

Brown, C., and Braithwaite, V. A. 2005. Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behavioural Ecology* 16: 482-487.

Brust, V., Krüger, O., Naguib, M., and Krause, E. T. 2014. Lifelong consequences of early nutritional conditions on learning performance in zebra finches (*Taeniopygia guttata*). *Behavioural Processes* 103: 320-326.

Buchanan-Smith, H. M., Anderson, D. A., and Ryan, C. W. 1993. Responses of cotton-top tamarins (*Saguinus oedipus*) to faecal scents of predators and non-predators. *Animal Welfare* 2: 17–32.

Burns, J. G. 2008. The validity of three tests of temperament in guppies (*Poecilia reticulata*). *Journal of Comparative Psychology* 122: 344-356.

Capitanio, J. P. 1999. Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation *American Journal of Primatology* 47(4): 299-320.

Carere, C., Drent, P. J., Koolhaas, J. M., and Groothuis, T. G. G. 2005. Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour* **142**: 1335–1361.

Carere, C. and Maestripieri, D. 2013. *Animal personalities: Behaviour, Physiology, and Evolution*. The University of Chicago Press, Chicago, USA.

Chiweshe, N. 2007. The current conservation status of the Southern Ground Hornbill Bucorvus leadbeateri in Zimbabwe. In: Kemp, A. C. & Kemp, M. I. (eds). The Active Management of Hornbills and their Habitats for Conservation, pp. 252-266. CD-ROM Proceedings of the 4th International Hornbill Conference, Mabula Game Lodge, Bela-Bela, South Africa. Naturalists & Nomads, Pretoria.

Cooper, M., and Jordan, L. 2013. Random time-activity budgets in captive Southern Ground Hornbill Bucorvus leadbeateri. *South African Journal of Science* 109(7/8): 1-2.

Daley, M. A., and Birn-Jeffery, A. 2018. Scaling of avian bipedal locomotion reveals independent effects of body mass and leg posture on gait. *Journal of Experimental Biology* 221: 1-13.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* 7: 734-739.

Derwent, S. & Mander, M. 1997. Twitchers bewitched: The use of birds in traditional healing. Africa - Birds and Birding. 2(1):22–25.

De Waal, F. B. M. 1989. The myth of a simple relation between space and aggression in captive primates. *Zoo Biology* 1: 141–148.

De Waal, F. B., Aureli, F., and Judge, P. G., 2000. Coping with crowding. *Scientific American* 282: 76–81.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., and Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* 76: 1128-1138.

Dingemanse N. J., Both C., Drent P. J., van Oers K., and van Noordwijk A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* **64**: 929–937.

Dingemanse, N. J., and Wolf. M. 2015. Recent models for adaptive personality differences: a review *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1560): 71-97.

Dingemanse, N. J., Both, C., Drent, P. J. and Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B* 271: 847–852.

Dingemanse, N. J., and Wolf, M. 2010. Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3947–3958.

Dingemanse, N. J., and Reale, D. 2005. Natural selection and animal personality. *Behaviour* 142:1159–1184.

Drent, P. J., Van Oers, K. and Van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society London* 270: 45–51.

Duckworth, R. A. 2006. Behavioural correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioural Ecology* 17: 1011-1019.

Duncan, L. M., Jones, M. A., van Lierop, M., and Pillay, N. 2013. Chimpanzees use multiple strategies to limit aggression and stress during spatial density changes. *Applied Animal Behaviour Science* 147(1–2): 159-171.

Finlay, T., James, L. R., and Maple, T. L. 1988. People's perceptions of animals: the influence of zoo environment. *Environment and Behaviour* 20: 508–528.

Forsberg, O. 1994. More Ground Hornbills. *Tiptol* 32:7.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. and Skalski, G. T. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist* 158: 124–135.

Fuller, T., Sarkar, S., and Crews, D. 2005. The use of norms of reaction to analyse genotypic and environmental influences on behaviour in mice and rats. *Neuroscience and Biobehavioral Reviews* 29: 445-456.

Gattermann, R., Johnston, R. E., Yigi, N., Fritzsche, P., Larimer, S., Özkurt, S., Neumann, K., Song, K., Colak, E., Johnston, J., and McPhee, E. M. 2008. Golden hamsters are nocturnal in captivity but diurnal in nature. *Biology letters* 4(3) 1-8.

Godin, J. G., and Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulate*. *Proceedings of the National Academy of Sciences USA* 93: 10262-10267.

Gosling, S. D. 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, 112(2): 107-118.

Gosling, S.D. 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin* 127: 45-86.

Hediger, H. 1970. *Man and Animal in the Zoo*. Routledge and Kegan Paul: London, UK.

Hemsworth, P. H. 2003. Human–animal interactions in livestock production. *Applied Animal Behaviour Science* 81(3): 185-198.

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander., L., and Arnold, K. E. 2010. Personality in captivity reflects personality in the wild. *Animal Behaviour* 79: 835–843

Hockley, M., and Archer, W. H. 1966. The Southern Ground Hornbill or "Bromvogel". *Cape Department of Nature Conservation Report.*

Hoff, M. P., Hoff, K. T., Horton, L. C., and Maple, T. L. 1996. Behavioural effects of changing group membership among captive lowland gorillas. *Zoo Biology* 15: 383–393.

Hosey, G. R. 2005. How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* 90: 107–129.

Houston, A. I., and McNamara, J. M. 1999. *Models of adaptive behaviour*. Cambridge, UK: Cambridge University Press. 6: 243–253

Hughes, R. N. 1997. Intrinsic exploration in animals: motives and measurement. *Behavioural Processes* 41: 213-226.

Huntingford, F. A., Wright, P. J., and Tierney, J. F. 1994. *Adaptive variation in antipredator behaviour in threespine stickleback. In The Evolutionary Biology of the Threespine Stickleback* (eds. M. A. Bell and S. A. Foster), pp. 345–380. Oxford University Press, New York.

Huntingford F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24:** 245–260.

IUCN. 2012a. Guidelines for application of IUCN Red List Criteria at regional and national levels: Version 4.0. Gland, Switzerland and Cambridge UK.

IUCN. 2012b. IUCN Species Survival Commission Guidelines on the Use of ex situ Management for Species Conservation.

IUCN 2019. The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org. Downloaded on 15 January 2019.

Kemp, A. C. 1995. *The Hornbills, Bucerotiformes*. Oxford University Press, Oxford.

Kemp, A. C. 2005. Southern Ground-Hornbill. In: Hockey, P.A.R., Dean, W.R.J. and Ryan, P. G. (eds), *Roberts – Birds of Southern Africa,* VIIth ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town. 158-159.

Kemp, A. C. 1976. Factors affecting the onset of breeding in African hornbills. *Proceedings of the 16th International Ornithological Congress* 248-257.

Kemp, A. C. 1988. The behavioural ecology of the Southern Ground Hornbill: are competitive offspring at a premium? In: *Proceedings of the International 100th DOG meeting, Current Topics in Avian Biology* 267-271.

Kemp, A. C. 2000. *Southern Ground Hornbill.* In: Barnes, K.N. (Ed). *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg*. Pp. 117-119.

Kemp, A. 1987. Ground Hornbill under pressure in South Africa. *African Wildlife* 41: 293.

Kemp, A. C. and Begg, K. S. 2001. Comparison of time-activity budgets and population structure for 18 large-bird species in the Kruger National Park, South Africa. *Ostrich* 72(3):179–184.

Kemp, A. C. and Kemp, M. I. 1980. The biology of the Southern Ground Hornbill *Bucorvus leadbeateri*. (Vigors) (Aves: *Bucerotidae*). *Annals of the Transvaal Museum* 32(4): 65-100.

Kemp, A. C. and Kemp, M. I. 1991. Timing of egg laying by Southern Ground Hornbills *Bucorvus leadbeateri* in the Kruger National Park, South Africa. *Ostrich* 62: 80-82.

Kemp, V. L. 2017. Conservation biology and molecular ecology of the Southern Ground-Hornbill *Bucorvus leadbeateri* (Vigors, 1825). Doctor of Philosophy (PhD). University of the Free State, Bloemfontein, South Africa.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation: guidelines for reintroducing captive endangered species into the wild. *Bioscience* 39(3): 152–161.

Kluen, E., Kuhn, S., Kempenaers, B., and Brommer, J. E. 2012. A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal Behaviour* 1-9.

Kortet, R., Sirkka, I., Lai1, Y. T., Vainikka, A, and Kekäläinen, J. 2015. Personality differences in two minnow populations that differ in their parasitism and predation risk. *Frontiers in Ecology and Evolution* 18: 19–34.

Kortet, R., Hedrick, A. V., and Vainikka, A. 2010. Parasitism, predation and the evolution of animal personalities. *Ecology letters* 13: 1449–1458.

Kurvers, R. H. J., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., and Prins, H. H. T. 2009. Personality differences explain leadership in barnacle geese. *Animal Behaviour* 78(2): 447-453.

Lukas, K. E., Hoff, M. P., and Maple, T. L. 2003. Gorilla behavior in response to systematic alternation between zoo enclosures. *Applied Animal Behaviour Science* 81: 367–386.

Macrì, S., Adriani, W., Chiarotti, F., and Laviola, G. 2002. Risk taking during exploration of a plus-maze is greater in adolescent than in juvenile or adult mice. *Animal Behaviour* 64(4): 541-546.

MacDonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301: 379-383.

Mackay, M. K. 2017. Behavioural adaptive variation in the striped mouse *Rhabdomys.* Doctor of Philosophy. University of the Witwatersrand, Johannesburg, South Africa.

Magnhagen, C., Wacker, S., Forsgren, E., Myhre, L. C., Espy, E. and Amundsen, T. 2014. Context Consistency and Seasonal Variation in Boldness of Male Two-Spotted Gobies. *PloS one* 9-10.

Mallapur, A., Sinha, A. and Waran, N. 2005. Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. App*lied Animal Behaviour Science* 94: 341–352.

Mallapur, A., and Chellam, R. 2002. Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in Southern India. *Zoo Biology* 21(6): 585-595.

Marliave, J. B., Gergits, W. F., and Aota, S. 1993. F10 pandalid shrimp: Sex determination; DNA and dopamine as indicators of domestication; and outcrossing for wild pigment pattern. *Zoo biology* 12(5): 435-451.

Martin, J. G. A., and Réale, D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus. Animal Behaviour* 75(1): 309-318.

Martin, P., and Bateson, P. 1993. *Measuring behaviour: an introductory guide, 2nd ed*. Cambridge University Press, Cambridge, UK.

Melfi, V. A., and Thomas, S. 2005. Can training zoo-housed primates compromise their conservation? A case study using Abyssinian colobus monkeys (*Colobus guereza*). *Anthrozoös* 18(3): 304-317.

Meshik, V.A., 1999. Introducing male ring-tailed lemurs. Int. Zoo News 46 (2), 86–90.

Mitchell, G., Herring, F., Obradovich, S., Tromborg, C., Dowd, B., Neville, L. E., and Field, L. 1991. Effects of visitors and cage changes on the behaviours of Mangabeys. *Zoo Biology* 10: 417-423.

Mowles, S. L., Cotton, P. A., and Briffa, M. 2012. Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology* 66(7): 1087–1094.

Morrison, K., Daly, B., Burden, D., Engelbrecht, D., Jordan, M., Kemp, A., Kemp, M., Potgeiter, C., Turner, A., and Friedmann, Y. (eds). 2005. Southern Ground Hornbill (Bucorvus leadbeateri) PHVA Workshop Report. Conservation Breeding Specialist Group (SSC / IUCN) / CBSG South Africa; Endangered Wildlife Trust, Johannesburg.

Morrison, K., Daly, B., Burden, D., Engelbrecht, D., Kemp, A., Kemp, M., Potgieter, C. and Turner, A. 2007. A conservation plan for the Southern Ground Hornbill *Bucorvus leadbeateri* in South Africa. In Proceedings of the 4th International Hornbill Conference: The Active Management of Hornbills and their Habitats for Conservation. A. C. Kemp and M. I. Kemp, Eds. Pretoria, South Africa: Naturalists and Nomads 3–12.

Niemela, P. T., Di Rienzo, N. and Hedrick, A.V. 2012. Predator-induced changes in the boldness of naive field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behaviour* 84: 129-135.

Nieuwenhuijsen, K., and de Waal, F. B. 1982. Effects of spatial crowding on social behaviour in a chimpanzee colony. *Zoo Biology* 1: 5–28.

Nimon, A. J., and Dalziel, F. R. 1992. Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. *Applied Animal Behaviour Science* 33: 261-272

Noldus Information Technology. 2013. *Ethovision XT: Noldus Information Technology*, the Netherlands.

O'Donovan, D., Hindle, J. E., McKeown, S., and O'Donovan, S. 1993. Effect of visitors on the behaviour of female cheetahs *Acinonyxjubatus*. *International Zoo Yearbook* 32: 238-244.

Øverli, Ø., Sørensen, C., and Nilsson, G. E. 2006. Behavioural indicators of stress-coping style in 584 rainbow trout: Do males and females react differently to novelty? *Physiology and Behaviour* 87: 506 – 512.

Patrick, S.C., and Weimerskirch, H. 2014. Personality, foraging and fitness consequences in a long lived seabird. *PLoS One* 9(2): 87-96.

Perkins, L. A., 1992. Variables that influence the activity of captive orangutans. *Zoo Biology* 11: 177–186.

Pervin, L. A., and John, O. P. 1999. *Handbook of personality: Theory and research*. Guilford Press, New York, New York, USA.

Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W., and Fritza, H. 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour* 79(3): 665-671.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. and Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82: 291-318.

Réale D., Gallant B. Y., Leblanc M., and Festa-Bianchet M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* **60**: 589–597.

Reinhardt, V., 1990. Social enrichment for laboratory primates: a critical review. *Laboratory Primate Newsletter* 29 (3): 7– 11.

Reinhardt, V., Liss, C., and Stevens, C., 1995. Social housing of previously single-caged macaques: what are the options and the risks? *Animal Welfare* 4: 307–328.

Reinhardt, V., Houser, D., Eisele, S., Cowley, D., Vertein, R. 1988. Behavioural responses of unrelated rhesus monkey females paired for the purpose of environmental enrichment *American Journal of Primatology* 14: 135–140.

Rhoads, D. L., and Goldsworthy, R. J., 1979. The effects of zoo environments on public attitudes toward endangered wildlife. *International Journal of Environmental Studies* 13(4): 283–287.

Riechert, S. E. and Hedrick, A.V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta (Araneae, Agelenidae). Animal Behaviour* 46(4): 669-675.

Seaman, B., and Briffa, M. 2015. Parasites and personality in periwinkles (*Littorina littorea*): Infection status is associated with mean-level boldness but not repeatability. *Behavioural Processes* 115: 132-134.

Seddon, P. J., Armstrong, D. P., and Maloney, R. F. 2007. Developing the Science of Reintroduction Biology. *Conservation Biology* 21(2): 303–312.

Seres, M., Aureli, F., de Waal, F. B. M., 2001. Successful formation of a large chimpanzee group out of two preexisting subgroups. *Zoo Biology* 20: 501–505.

Sih, A., and Bell, A. M. 2008. Insights for behavioural ecology from behavioural syndromes. *Advances in the Study of Behaviour* **38**: 227–281.

Sih, A., Bell, A. M., and Johnson, J. C. 2004a. Behavioural syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19: 372-378.

Sih, A., Kats, L. B., and Maurer, E. F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour* 65(1): 29-44.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P. O., Wolf, M., and Dingemanse, N. J. 2015. Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology and Evolution* 30(1): 50-60.

Sih A., Bell A. M., Johnson J. C., and Ziemba R. E. 2004b. Behavioural syndromes: an integrative overview. *The quarterly review of Biology* **79**: 241–277.

Silber, S. Joshi, S and Pillay, N. 2019. Behavioural syndromes in stereotypic striped mice. *Applied Animal Behaviour Science*. In press.

Sinn, D. L., and Moltschaniwskyj, N. A. 2005. Personality traits in dumpling squid (*Euprymna tasmanica*): Context-specific traits and their correlation with biological characteristics. *Journal of Comparative Psychology* 119: 99–110.

Sinn D. L., Moltschaniwskyj N. A., Wapstra E., and Dall S. R. X. 2010. Are behavioural syndromes invariant? Spatiotemporal variation in shy/bold behaviour in squid. *Behavioural Ecology and Sociobiology* 64(4): 693–702.

Southwick, C., Siddiqi, M. F. 1998. *The rhesus monkeys fall from grace. In: Ciochon, R.L., Nisbett, R.A. (Eds.), The Primate Anthology*. Prentice Hall, New Jersey, pp. 211–218.

Stamps, J. A., and Groothuis, T. G. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B* 365: 4029-4041.

Tarboton, W. R. 1980. Avian populations in Transvaal savanna. In: Johnson, D.N. (Ed). Proceedings of the 4th Pan-African Ornithological Congress. Southern African Ornithological Society, Johannesburg. Pp. 113-124.

Taylor, M., and Kemp, L. 2015a. Southern Ground-Hornbill *Bucorvus leadbeateri*. *In The 2015 Eskom Red Data Book of Birds* 119–121.

Taylor, M. R., and Kemp, L. V. 2015b. Southern Ground-Hornbill. In The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. M.R. (ed). Taylor, Ed. Johannesburg, South Africa: BirdLife South Africa.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185-207.

Theron, N., Jansen, R., Grobler, P., and Kotze, A. 2011. Home range of a recently established group of southern ground hornbill (*Bucorvus leadbeateri*) outside of formally protected areas in the Limpopo Valley, South Africa. *Koedoe* 55(1).

Thompson, V. D. 1989. Behavioural response of 12 ungulate species in captivity to the presence of humans. *Zoo Biology* 8: 275-297.

Torgerson-White, L. L., and Bennett, C. 2014. Rating methodology, personality axes, and behavioural plasticity: A case study in African lions. *Animal Behaviour and Cognition* 1(3): 230-248.

Trail, P. W. 2007. African hornbills: keystone species threatened by habitat loss, hunting and international trade. *Ostrich* 78(3):37–41.

Trut, L. N. 1999. Early canid domestication: the farm-fox experiment. *American Scientist* 87: 160–169.

Van Oers, K., Drent, P. J., Dingemanse, N. J. and Kempenaers, B. 2004. Personality is associated with extrapair paternity in great tits, *Parus major*. *Animal Behaviour* 76(3): 555-563

Verbeek M. E. M., Boon A. and Drent P. J. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* **133**: 945–963.

Vervaecke, H., Stevens, J. M. G. Vandemoortele, H., Sigurjónsdóttir, H., and Vries, H. D. 2007. Aggression and dominance in matched groups of subadult Icelandic horses (*Equus caballus*) *Journal of Ethology* 25(3): 239–248

Vernon, C. J. 1986. The Ground Hornbill at the southern extremity of its range. *Ostrich* 57: 16–24

Vernon, C. J. and Herremans, M. 1997. Ground Hornbill, *Bucorvus leadbeateri*. Pp. 708–709 in J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker and C. J. Brown, eds. Atlas of Southern African birds. Vol. 1: Non-passerines. Johannesburg: BirdLife South Africa.

Vigors. 1825. Conservation biology and molecular ecology of the Southern Ground-Hornbill *Bucorvus leadbeateri* (Aves: *Bucerotidae*). *Annals of the Transvaal Museum* 32(4): 65-100

White, B. C., Houser, L. A., Fuller, J. A., Taylor, S., Elliott, J. L. L. 2003. Activity-based exhibition of five mammalian species: evaluation of behavioural changes. Zoo Biology 22: 269–285.

Wilson, S. F., 1982. Environmental influences on the activity of captive apes. *Zoo Biology* 1: 201–209.

Wilson, D. S., Coleman, K., Clark, A. B. and Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology* 107: 250-260.

Wilson D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **353:** 199–205.

Wolf, M., and Weissing, F. J. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution* 27: 452-461.

Wolf, M., and Weissing, F. J. 2010. An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3959–3968.

Wolf, M., van Doorn, G. S., and Weissing F. J. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Science USA* **105:** 15825–15830.

Wilson, D. S., Coleman, K., Clark, A. B., Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. Journal of comparative Psychology 107(3): 250-260.

Wray, M. K., Mattila, H. R., and Seeley, T. D. 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Animal Behaviour* 81(3): 559-568.

Yuen, C. H., Pillay, N., Heinrichs, M., Schoepf, I., and Schradin, C. 2016. Personality traits are consistent when measured in the field and in the laboratory in African striped mice (*Rhabdomys pumilio*). *Behavioral Ecology and Sociobiology* 70: 1235-1246.

Yuen, C. H., Pillay, N., Heinrichs, M., Schoepf, I., and Schradin, C. 2015. Personality does not constrain social and behavioural flexibility in African striped mice. *Behavioral Ecology and Sociobiology* 69: 1237-1249.

Zoghby, B. A. 2015. Fine-scale movements and habitat use of the Southern Ground Hornbill *Bucorvus Leadbeateri.* MSc dissertation. University of Cape Town, Western Cape, South Africa.